STATE OF CALIFORNIA

Energy Resources Conservation and Development Commission

In the Matter of:

APPLICATION FOR CERTIFICATION
FOR THE IVANPAH SOLAR
ELECTRIC
GENERATING SYSTEM

DOCKET NO. 07-AFC-5

DOCKET
07-AFC-5
DATE DEC 17 2009
RECD. DEC 17 2009

OPENING TESTIMONY FOR TOPICS TO BE HEARD IN JANUARY, 2010 *EXHIBIT LIST, EXHIBITS, AND PROOF OF SERVICE* INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY

December 17, 2009

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STATE OF CALIFORNIA
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INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY
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INTRODUCTION

Pursuant to the Revised Notice of Prehearing Conferences and Evidentiary Hearing issued November 23, 2009, Intervenor Center for Biological Diversity (the "Center") provides this Opening Testimony for Topics to be Heard in January, 2010.

All of the testimony presented herein was prepared by the person testifying, a signed declaration and resume has also been provided for each person.

Center Attorney Lisa T. Belenky assisted in compiling this testimony and the documents submitted. A complete Exhibit List and copies of the documents are also being submitted with this testimony.

The Center for Biological Diversity reserves the right to supplement and/or revise this testimony at any time up to and including the close of the evidentiary hearings. Moreover, many of the factual issues discussed in this Opening Testimony involve both legal and factual questions while others are predominately legal issues. Therefore, the Center respectfully reserves the right to address all disputed issues identified at the hearings through testimony, rebuttal, cross-examination, or at later stages of this process including in briefing following the evidentiary hearing.

In addition to the statements herein, this testimony incorporates by reference the information in the following documents previously submitted in this proceeding:

1. July 8, 2009: RE: Application for Certification for the Ivanpah Solar Electric Generating System Docket No. 07-AFC-5: Comments on Staff Report for the Preliminary Staff Assessment December 2008 (07-AFC-5) CEC-700-2008-013-PSA – Ivanpah Solar Electric Generating System and the Draft Desert Tortoise Translocation/Relocation Plan and exhibits (also being re-submitted as document number 913)

2. November 16, 2009: PRELIMINARY PREHEARING CONFERENCE STATEMENT OF INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY

TESTIMONY SUBMITTED

1. **Testimony of Curtis Bradley, Re: Project Description/Environmental Setting/Alternatives for the Proposed Ivanpah Solar Electric Generating System, Declaration, Resume**

2. **Testimony of Mark C. Jorgensen, Re: Impacts to Bighorn Sheep from the Proposed Ivanpah Solar Electric Generating System, Declaration, and Resume**

3. **Testimony of Bill Powers, P.E., Regarding Alternatives, Declaration, Resume**

4. **Testimony of Ileene Anderson Re: Impacts to Sensitive Wildlife from the Proposed Ivanpah Solar Electric Generating System, Declaration, and Resume**

EXHIBIT LIST

Doc. No.	Author and title
900	Dodd, C.K. and R.A. Siegel 1991. Relocation, repatriation and translocation of amphibians andreptiles: are they conservation strategies that work? Herpetologica 47(3): 336-350.
901	Epps, C.W., P.J. Palsboll, J.D. Wehausen, G.K. Roderick, R.R. Ramey II, and D.R. McCullough 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letter 8: 1029-1038.
902	Epps, C.W., D. R. McCullough, J.D. Wehausen, V. C. Bleich and J.L. Rechel 2004. Effects of Climate Change on Population Persistence of Desert-Dwelling Mountain Sheep in California. Conservation Biology 18 (1): 102-113.
903	Field, K.J., C. R. Tracy, P.A. Medica, R.W. Marlow, and P.S Corn 2007. Return to the wild: Translocation as a tool in conservation of the desert tortoise (Gopherus agassizii). Biological Conservation 136: 232-245.
904	Frid, A. and L. Dill 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6(1): 11. "
905	Hiatt, H.D., T.E. Olson, J.C. Fisher. 1995. Reseeding four sensitive plant species in California and Nevada. in Proceedings: Wildand Shrub and Arid Land Restoration Symposium. General Technical Report INT-GTR-315. Pgs. 94-99."
906	Karl, A. E. 2007. Hyundai Motor America Mojave Proving Grounds, Desert Tortoise Translocation Study – 2006 Annual Summary. March 2007. Pgs. 20.
907	Lovich, J.E. and R. Daniels 2000. Environmental characteristics of desert tortoise (Gopherus agassizii) burrow locations in an altered industrial landscape. Chelonian Conservation and Biology 3(4): 714-721.

908 Luckenbach, R. A. 1985. Ecology and management of the desert tortoise (Gopherus agassizii) in California. In R. B. Bury ed., Ecology and conservation of North American tortoises. U.S. Fish and Wildlife Service Research Report 12. Pgs 1-37.

909 Murphy, R.W., K.H. Berry, T. Edwards, A.M. McLuckie. (2007) A Genetic Assessment of the Recovery Units for the Mojave Population of the desert tortoise (Gopherus agassizii). Chelonian Conservation and Biology 6(2): 229-251.

910 Palmer, K.S., D.C. Rostal, J.S. Grumbles, M. Mulvey. 1998. Long-term sperm storage in thedesert tortoise (Gopherus agassizii). Copiea 3:702-705.

911 Deacon, James E., Williams, A.E., Williams, C.D., and Williams, J.E.; September 2007, Fueling Population Growth in Las Vegas: How Large-scale Groundwater Withdrawal Could Burn Regional Biodiversity, BioScience Vol. 57 No. 8 688-698

912 McCrary et al., Avian Mortality at a Solar Energy Power Plant, J. Field Ornithol., 57(2): 135-141. 1986. Solar One 4 km east of Daggett, San Bernardino County, California.

913 CBD letter to CEC RE: Comments on Preliminary Staff Assessment December 2008 (07-AFC-5) CEC-700-2008-013-PSA – Ivanpah Solar Electric Generating System and the Draft Desert Tortoise Translocation/Relocation Plan dated May 26, 2009.

914 Lovich, J. E., and D. Bainbridge. 1999. Anthropogenic Degradation of the Southern California Desert Ecosystem and Prospects for Natural Recovery and Restoration. Environmental Management Vol. 24, No. 3, pp 309-326

915 Brown, D.E. and R. A. Minnich. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. American Midland Naturalist Vol. 116: 411-422

916 Walker, L.R., D.B. Thompson, and F.H. Landau 2001. Experimental manipulations of fertile islands and nurse plant effects in the Mojave desert, USA. Western North American Naturalist 61(1): 25–35.

917 Brooks, M.L. 2000. Competition Between Alien Annual Grasses and Native Annual Plants in the Mojave Desert. Am. Midl. Nat. 144:92–108"

918 Brooks, M. L. and J. V. Draper. 2006. Fire effects on seed banks and vegetation in the Eastern Mojave Desert: implications for post-fire management, extended abstract, U.S. Geological Survey, Western Ecological Research Center, Henderson, Nevada, 3 p.

919 Brooks, M.L. and R.A. Minnich. In Press. Fire in the Southeastern Deserts Bioregion. Chp 16 in: Sugihara, N.G., J.W. van Wagtendonk, J. Fites-Kaufman, K.E. Shaffer and A.E. Thode (eds.). Fire in California Ecosystmes. University of California Press, Berkeley.

920 Dutcher, K. E. 2009. The effects of wildfire on reptile populations in the Mojave National Preserve, California. Final Report to the National Park Service, California State University, Long Beach, 28 p.

921 Beck, D.D. 1990. Ecology and Behavior of the Gila Monster in Southwestern Utah. Journal of Herpetology, Vol. 24, No. 1 (Mar., 1990), pp. 54-68

922 Sullivan, B.K., M.A. Kwiatkowski and G.W. Schuett. 2004. Translocation of urban Gila monsters: a problematic conservations tool. Biological Conservation 117: 235-242

923 B. Murphy – Fulcrum Technologies, Inc., The Power and Potential of CdTe (thin-film) PV, presented at 2nd Thin-Film Summit, San Francisco, December 1-2, 2009.

924 Schreiber, D. - EuPD Research, PV Thin-film Markets, Manufacturers, Margins, presentation at 1st Thin-Film Summit, San Francisco, December 1-2, 2008.

925 CPUC Rulemaking R.06-02-012, Develop Additional Methods to Implement California RPS Program, Pre-Workshop Comments of GreenVolts, Cleantech America, and Community Environmental Council on the 2008 Market Price Referent, March 6, 2008,

926 E-mail communication between Don Kondoleon, manager - CEC Transmission Evaluation Program, and Bill Powers of Powers Engineering, January 30, 2008

927 SCE Application A.08-03-015, Solar Photovoltaic (PV) Program Supplemental Rebuttal Testimony, October 14, 2008

928 Camp et al. 1997, Viewsheds: a complimentary management approach to buffer zones, Wildlife Society Bulletin 1997, 25(3):612-615

929 Goodrich and Buskirk 1998. SPACING AND ECOLOGY OF NORTH AMERICAN BADGERS (TAXIDEA TAXUS) IN A PRAIRIE-DOG (CYNOMYS LEUCURUS) COMPLEX, Journal of Mammalogy, 79(1):171-179, 1998

930 Klem 1989 Bird window collisions, Wilson Bull., 101(4), 1989, pp. 606-620

931 Long 1973. Taxidea taxus, Mammalian Species, No. 26, Taxidea taxus (Jun. 13, 1973)

932 Longcore 1997 On the Perils of Ecological Restoration: Lessons from the El Segundo Blue Butterfly; In press, 2nd Interface Between Ecology and Land Development in California J.E. Keeley, Coordinator. Occidental College, April 18-19, 1997.

933 Richardson and Miller 1997. Recommendations for protecting raptors from human disturbance: a review, Wildlife Society Bulletin 1997, 25(3):634-638

Dated: December 17, 2009

Respectfully submitted,

Lisa T. Belenky

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STATE OF CALIFORNIA

Energy Resources Conservation and Development Commission

In the Matter of: APPLICATION FOR CERTIFICATION FOR THE IVANPAH SOLAR ELECTRIC GENERATING SYSTEM	DOCKET NO. 07-AFC-5

INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY

Testimony of Curtis Bradley

Re: Project Description/Environmental Setting/Alternatives for the Proposed Ivanpah Solar Electric Generating System

Docket 07-AFC-5

Qualifications

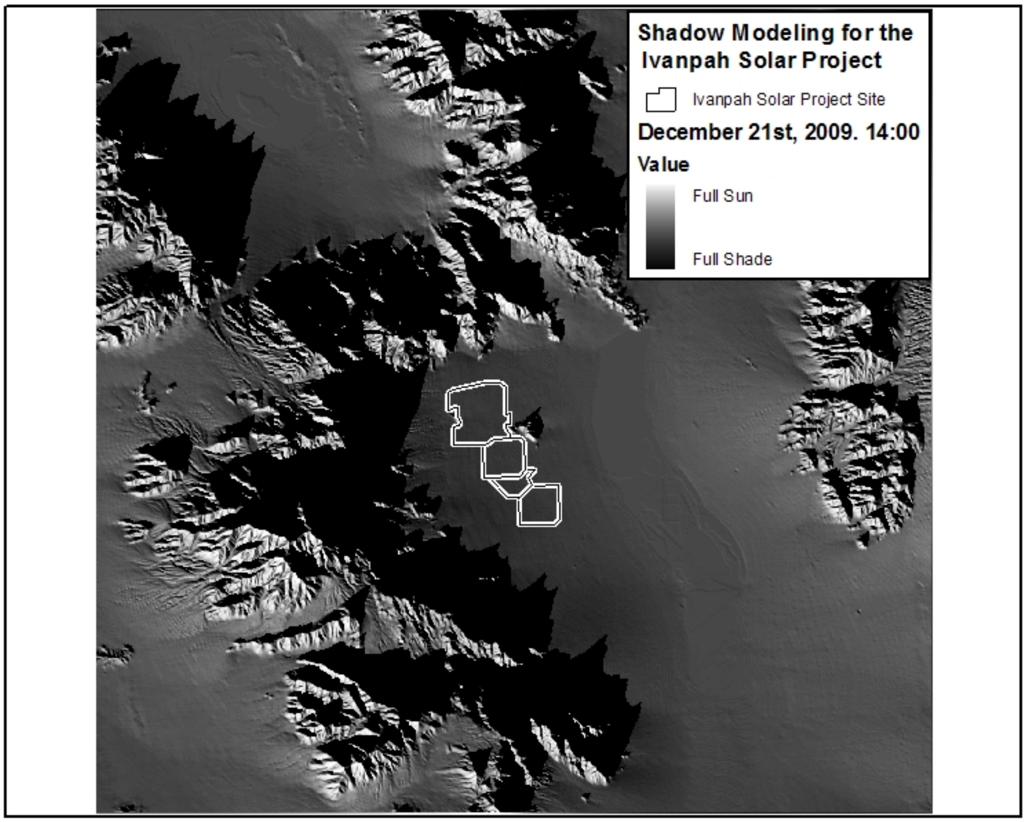
My qualifications are provided on my Resume attached to this Testimony and as discussed below.

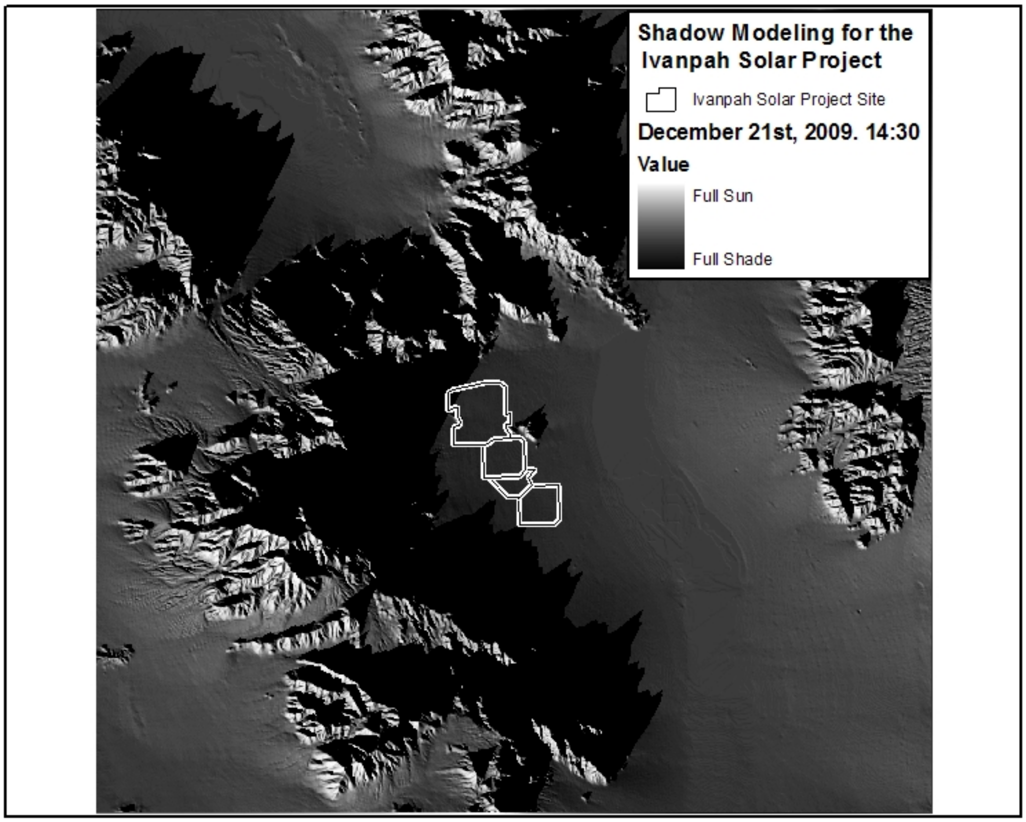
I am the Geographic Information Systems (GIS) specialist at the Center for Biological Diversity. I hold a Bachelor of Sciences in mechanical engineering and a Master of Sciences in watershed management, both from the University of Arizona. I have training in several GIS software applications and over 10 years of experience in GIS analysis and cartography.

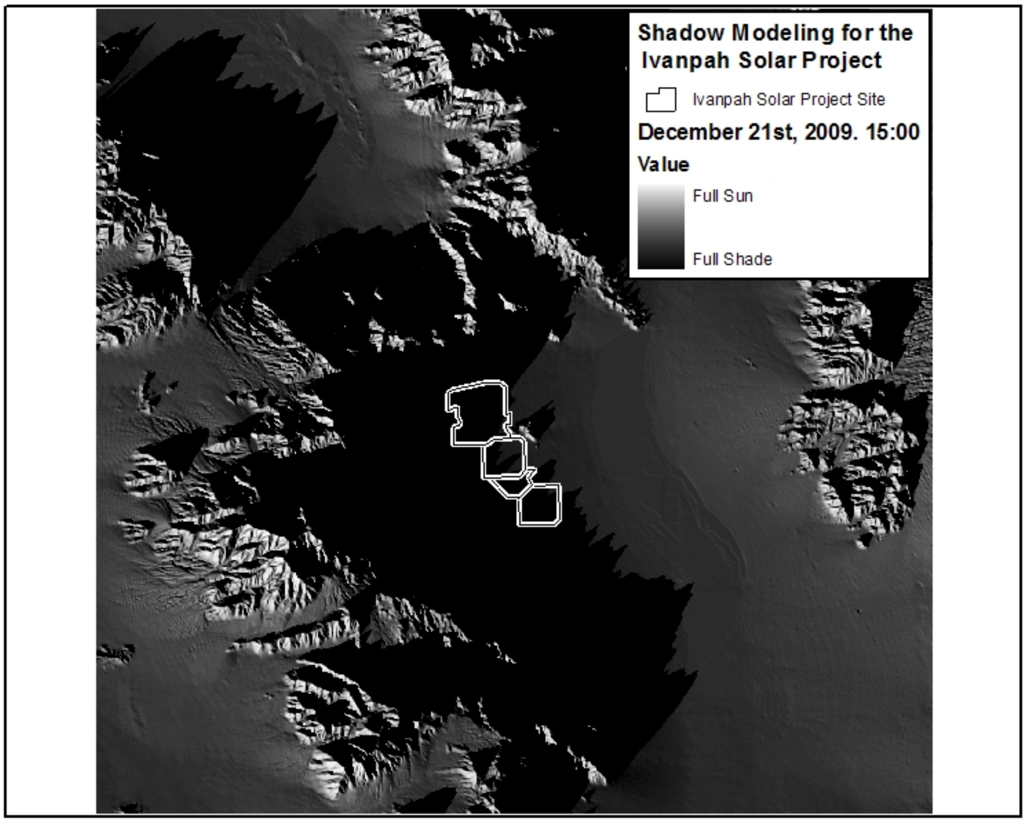
I prepared the maps below showing mountain shadows on the proposed Ivanpah solar site using GIS data and GIS software. I digitized (created a digital map of) the boundaries of the Ivanpah project from the project maps in the record. This allowed me to determine the longitude and latitude of the project site. I then entered these coordinates in the Astronomical Applications Department of the U.S. Naval Observatory website http://aa.usno.navy.mil/data/docs/AltAz.php. This website calculates the sun's altitude and azimuth for any given time and day of the year.

I used the altitude and azimuth information in my GIS software package, ArcGIS 9.3 (ESRI, 1999–2009), to create the shadow maps. This was done using the hillshade command in the spatial analyst extension with the ‘model shadows’ checkbox on using a 30 meter digital elevation model downloaded from the U.S. Geological Survey as the input surface. The resulting maps show the shadows at sunrise and sunset for summer and winter solstices along with the boundaries of the project.

Maps of Mountain Shadows on the Proposed Project Site




Shadow Modeling for the Ivanpah Solar Project
Ivanpah Solar Project Site
December 21st, 2009. 14:30
Value
Full Sun
Full Shade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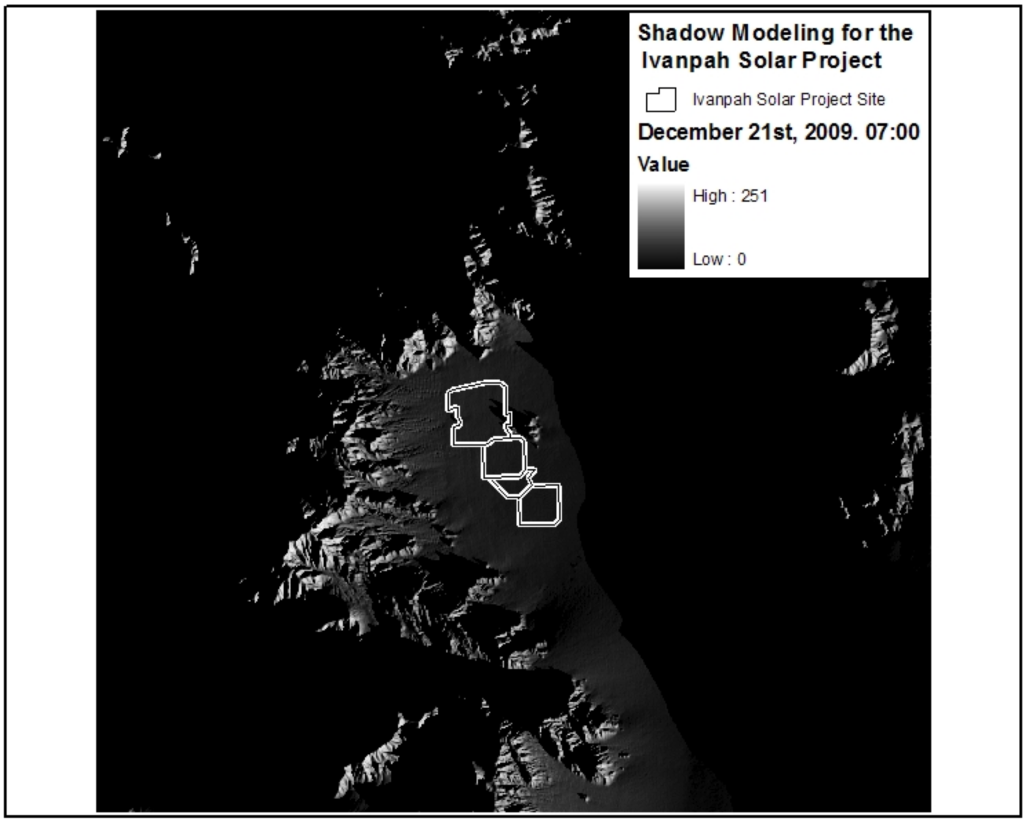
Value
Full Sun
Full Shade


Shadow Modeling for the Ivanpah Solar Project
Ivanpah Solar Project Site
December 21st, 2009. 07:00
Value
High : 251
Low : 0


Shadow Modeling for the Ivanpah Solar Project
Ivanpah Solar Project Site
June 21st, 2010. 17:00
Value
High : 254
Low : 0


Shadow Modeling for the Ivanpah Solar Project
Ivanpah Solar Project Site
June 21st, 2010. 17:30
Value
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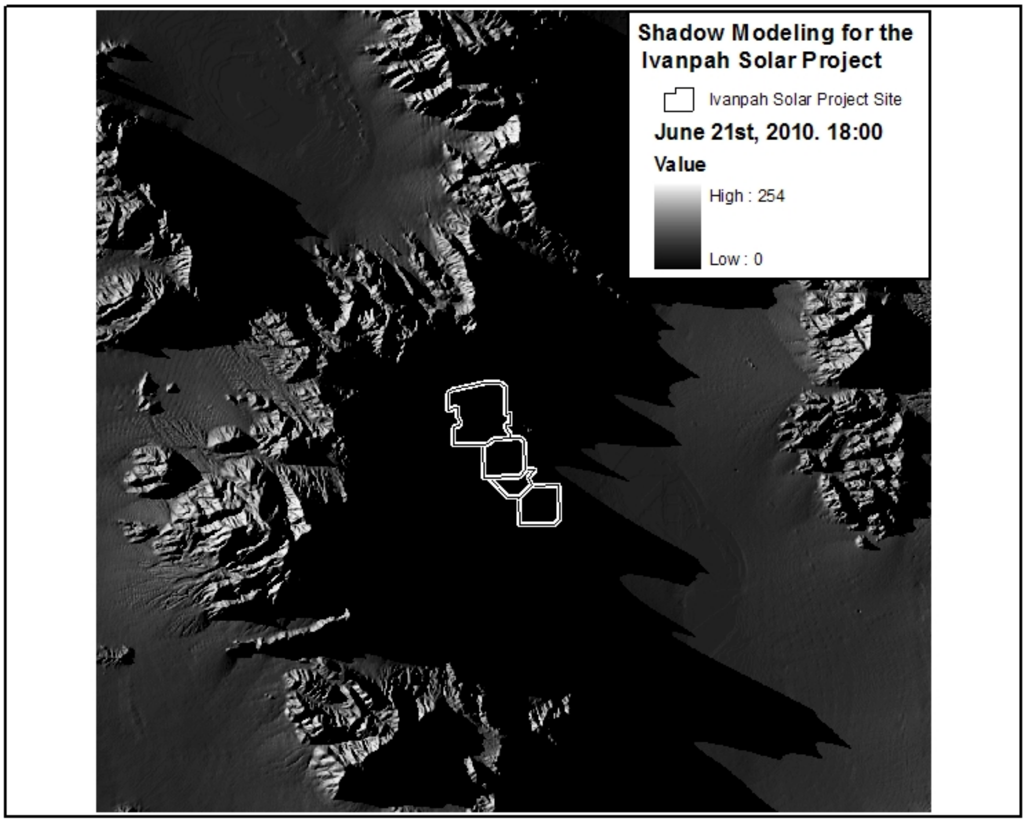
Low : 0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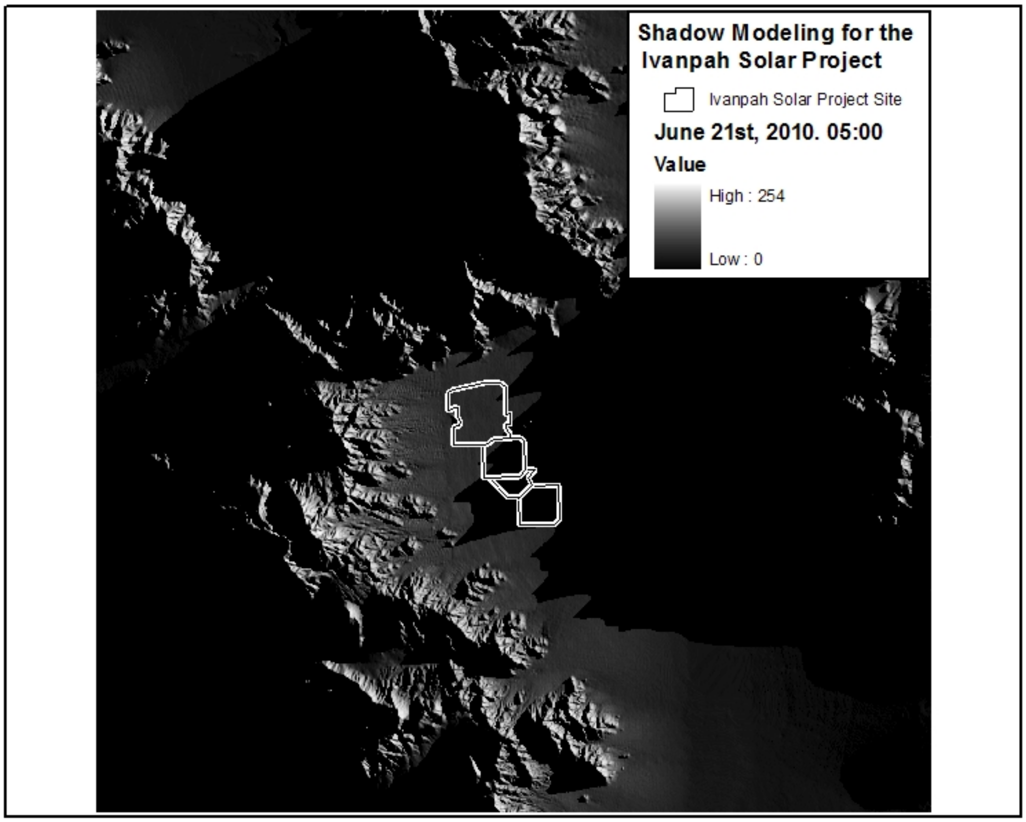
Shadow Modeling for the Ivanpah Solar Project
Ivanpah Solar Project Site
June 21st, 2010. 05:00
Value
High : 254
Low : 0

Declaration of Curtis Bradley

Re: Mountain Shadows on the Proposed Ivanpah Solar Electric Generating System

Docket 07-AFC-5

I, Curtis Bradley, declare as follows:

1) I am currently employed as the GIS Specialist at the Center for Biological Diversity, a position I have held for 9 years.

2) My relevant professional qualifications and experience are set forth in the attached resume and the attached testimony and are incorporated herein by reference.

3) I prepared the testimony and maps attached hereto and incorporated herein by reference, relating to the impacts of the Project on bighorn sheep.

4) I prepared the testimony and maps attached hereto and incorporated herein by reference relating to the proposed Project in the Ivanpah Valley in San Bernardino County.

5) It is my professional opinion that the attached testimony and maps are true and accurate with respect to the issues that they address.

6) I am personally familiar with the facts and conclusions described within the attached testimony and if called as a witness, I could testify competently thereto.

I declare under penalty of perjury that the foregoing is true and correct to the best of my knowledge and belief.

Dated: December 14th , 2009 Signed: ______________________

At: Tucson, Arizona

Curtis M Bradley

Profile:

- GIS project manager that solves unique problems daily.

Relevant Experience and Accomplishments:

GIS/Geography Experience

- Produced hundreds of cartographic products.
- Managed and supervised several individuals.
- Extensive use of ArcInfo, ArcView and digital orthographic images for map production and correction.

Employment History:

Jan 2001 – Present. GIS Specialist,
Center for Biological Diversity, Tucson, Arizona.
Managed databases, produced cartographic products, charts, reports, graphics and performed spatial analysis for a staff of over 60 scientists and attorneys including spatial database design, population, programming, and digitizing.

Dec 2006 - Present. Information Technology Director,
Center for Biological Diversity, Tucson, AZ.
Performed and supervised in house technical support of all computer and phone systems for staff. Performed software and hardware upgrades and purchases and directed dutes including help desk support.

June 1999 – Jan 2001. GIS Specialist,
Sky Island Alliance, Tucson, Arizona
Produced maps, edited, managed databases of the Sky Island Wildlands Network and proposed wilderness of Southeast Arizona.

Education and Training:

Masters of Science, Watershed Management
University of Arizona, AZ. 2003.

Bachelor of Science, Mechanical Engineering
University of Arizona, AZ. 1992

Microsoft Certified Systems Engineer, 1999.

GIS Software:

ArcGIS 9.x, 8.x, ArcToolBox, ArcCatalog, other functionalities of ArcGIS 9.x
ArcView 3.x, ArcINFO 7.x, ArcINFO
3D, Network, and Spatial Analyst(s), ArcIMS

Programming/Databases/Other:

ArcINFO with AMLs, Visual Basic for Applications.
MS Excel, MS Access., Python scripting

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INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY

Testimony of Mark C. Jorgensen

Re: Impacts to Bighorn Sheep from the Proposed Ivanpah Solar Electric Generating System

Docket 07-AFC-5

Qualifications

My qualifications are provided on my Resume attached to this Testimony and as discussed below.

I recently retired from my position as State Park Superintendent at Anza-Borrego Desert State Park, a position I held for 8 years. In my capacity as State Park Superintendent I was responsible for management and preservation of Peninsular bighorn sheep herds that inhabit the Park.

My bighorn work began as a teenager. I observed my first bighorn in 1967 in Chino Canyon, at Palm Springs. In 1972 I was hired by Anza-Borrego Desert State Park for four summers to conduct field research for CA State Parks. I have coordinated the annual desert bighorn sheep count for Anza-Borrego since 1972, the longest continuous annual census of desert bighorn.

In 1987 I coordinated the removal of about 150 feral cattle from bighorn habitat in Anza-Borrego, followed by the 2003 removal of 29 feral horses for the Park.

Beginning in 1992 I was part of the coordinated interagency effort to research desert bighorn, mountain lions, and mule deer in the Peninsular Ranges of San Diego, Riverside, and Imperial counties. Participating agencies included CA State Parks, CA Dept. of Fish & Game, UC Davis Wildlife Health Center, and US Fish & Wildlife Service.

I worked as a member of the Federal Recovery Team for Bighorn Sheep of the Peninsular Ranges under the direction of the USF&WS from its inception until 2008. I worked on the Recovery Team to develop the Recovery Plan and to delineate Critical Habitat for the long-term recovery of the Peninsular Ranges bighorn metapopulation.

Since 2006 I have been working with the Denver Zoological Foundation and the Mongolian Academy of Science to assist with the protection of Argali Sheep and Siberian Ibex in the Ikh Nartiin Chuluu Nature Reserve in the Gobi Desert of eastern Mongolia.

I have extensive experience in bighorn sheep habitat restoration, radio and GPS telemetry, bighorn capture and restraint techniques, wildlife corridors, bighorn water system construction and maintenance, and exotic plant and animal eradication to restore bighorn habitat. I have assisted many researchers and graduate students in projects pertaining to desert bighorn sheep, including habitat requirements, bighorn diseases, impacts of feral horses, sheep habitat modeling, Critical Habitat designation, population dynamics of the Peninsular Ranges, and bighorn habitat restoration. I have coauthored numerous published papers on the subjects enumerated above.

Statement

After my review of the bighorn sections of the FSA, my conclusion is that it does not comprehensively assess the impacts from of the proposed Project on the local bighorn population and the proposed mitigation measures do not address the impacts of the proposed Project on bighorn. In addition, there is no information provided in the document showing that there is a need for the proposed wildlife drinker as a mitigation measure. Is the Clark range lacking in available water sources accessible to bighorn sheep? No information is documented in the FSA.

There is a paucity of analysis or mitigation in regards to desert bighorn sheep. I find the review of bighorn impacts and suggested resolutions to be entirely unsatisfactory. Without this basic information about the use of the area by bighorn it is impossible to assess the extent of the impacts to the bighorn population in this area from the proposed Project.

The documents seem to indicate that the staff believes that all the potential bighorn impacts can be resolved by simply constructing one wildlife drinker system in the Clark Mountains. This does absolutely nothing to mitigate for the loss of forage areas, movement corridors, or the fragmentation of the habitat by constructing a massive solar operation in a wildlife corridor.

For many species addressed in the document the mitigation involves the purchase and future protection of an equal amount of acreage that is being impacted. No such suggestion is listed for bighorn, nor would the purchase elsewhere do anything for the movement corridor between the Clarks and the State Line Hills. Even if it is eventually constructed, the proposed bighorn water system as mitigation does nothing to make up for 4,000 acres of habitat being eliminated. As a result, the mitigation measure proposed does not relate to the loss of alluvial fan habitat where the Project would be constructed.

I suggest that a field study be conducted by a knowledgeable researcher in the Clark Mts. and on the proposed solar site, and probably on the State Line range as well. Absent any real information in the field, any suggested mitigation or perceived impacts are pure conjecture.

The documents concentrate on construction high on the alluvial fan, against the Clark Mountains. I see little to no discussion of considering the project at the bottom of the alluvial fan, along Interstate 15, and further away from bighorn foraging habitat.

I also note that similar concerns were raised in a letter dated October 27, 2009, the California Department of Fish and Game which nonetheless provided some proposed minimization measures. Letter from Kevin Hunting, page 4, "Comments on the Preliminary Staff Assessment and Recommendations for the Final Staff Assessment for the Ivanpah Solar Electric Generating System (CEC Docket # 07-AFC-5)". Although these measures may not be sufficient they could help reduce some of the impacts to bighorn and it is hard to understand why they were not discussed in the FSA. The measures include " moving back the fence at the base of the mountain range, not using barbed wire fencing in this location, checking known big horn sheep springs data periodically to ensure the Project wells are not adversely impacting sheep watering locations, and ensuring invasive plants have not taken over the springs are valid minimization measures that should be evaluated."

In summary, I find the document to be sorely lacking as it pertains to bighorn sheep. Jaeger and Wehausen are mentioned as references in the document that the staff had personal communications with. I believe it would be very beneficial to have them involved in a site-specific analysis and in formulating measures to avoid impacts to the bighorn and/or develop mitigation measures for the benefit of the local desert bighorn populations.

Declaration of Mark C. Jorgensen

Re: Impacts to Bighorn Sheep from the Proposed Ivanpah Solar Electric Generating System

Docket 07-AFC-5

I, Mark C. Jorgensen, declare as follows:

1) I am currently retired. I recently retired from my position as State Park Superintendent at Anza-Borrego Desert State Park, a position I held for 8 years.

2) My relevant professional qualifications and experience are set forth in the attached resume and the attached testimony and are incorporated herein by reference.

3) I prepared the testimony attached hereto and incorporated herein by reference, relating to the impacts of the Project on bighorn sheep.

4) I prepared the testimony attached hereto and incorporated herein by reference relating to the proposed Project in the Ivanpah Valley in San Bernardino County.

5) It is my professional opinion that the attached testimony is true and accurate with respect to the issues that they address.

6) I am personally familiar with the facts and conclusions described within the attached testimony and if called as a witness, I could testify competently thereto.

I declare under penalty of perjury that the foregoing is true and correct to the best of my knowledge and belief.

Dated: December 14, 2009

At: Borrego Springs, CA

Signed:

RESUME

Mark C. Jorgensen
Post Office Box 7
Borrego Springs, CA 92004-0007
760 625 5837--Cell

Present Position

Retired Annuitant, Environmental Scientist
Colorado Desert District

Retired (June 30, 2009)
State Park Superintendent III
Anza-Borrego Desert State Park

Education

California State University, Sacramento 1971-1973
Bachelor of Sciences Degree
Environmental Resources (Park Management)

Curriculum: Park Administration, Park Concepts, Ecology, Interpretation, Mammalogy, Geology, Geomorphology, Journalism, Park Law Enforcement, Historic Sites of CA, 14 Units of Special Studies in National and State Parks, Native Americans of California.

Grossmont Junior College 1969-1971

Curriculum: Vertebrate Zoology, Botany, Oceanography, History of CA, Latin American History, Conservation, Cultural and Physical Anthropology, Media, Public Speaking, Meteorology.

Imperial Valley College 1978-1979
Curriculum: Vertebrate Paleontology Two Semesters

Continuing Education:
FBI Firearms Instructor School, San Luis Obispo
Environmental Education for School Teachers, Yosemite Institute
Advanced Driver's Training, Los Angeles County Sheriff's Office
Course Leader Training, Asilomar
Time Management, San Diego Adult Education
Audubon Desert Institute, Tucson, AZ
Teaching English as a Second Language, San Diego State University
State Peace Officer Training, 25 weeks, Mott Training Center, Monterey, CA

Membership in Organizations

Desert Bighorn Council, Inc. Member, Technical Staff, former Chairman
Bighorn Institute, Advisor
Anza Borrego Foundation
Desert Protective Council
Former Charter Member, Federal Recovery Team for Peninsular Bighorn Sheep

Special Assignments

1976	Represented DPR in Sonora, Mexico at Desert Bighorn Council.
1978	Authored a ten part series for Ventura Star Free Press for 50th Anniversary of State Parks.
1981-1982	Training & Development Assignment as State Park Naturalist at Anza-Borrego.
1981-2005	Member of Flat-Tailed Horned Lizard Technical Advisory Committee with BLM, CDF&G, USF&WS, and USN.
1982-1998	Instructor and Assistant Program Coordinator, Mott Training Center Interpreting Natural History, Resource Management, and Cadet Academy.
1982	Facilitator for DPR Director's "Mission 1990" in Southern CA.
1982	Submitted State Wilderness proposal to SP Comm. for 282,000 acres in Anza-Borrego.
1983	Consultation and Field Survey of Henry W. Coe SP on Wilderness Proposal. Submitted maps and proposal to Director. State Wilderness was subsequently designated.
1983-1984	Assigned to committee by Senator Robert Presley to work on issues of land ownership and resource protection in Santa Rosa Mountains.
1984	Cooperative international wildlife project with the State of Sonora, Mexico to capture bighorn sheep for Centro Ecologico del Desierto in Hermosillo, Sonora.
1984-1985	Consultant to the Kingdom of Saudi Arabia, Riyadh Development Authority, for development of a plan for 80,000 acre Thumamah Nature Park in Central Saudi Arabia.
1982-Pres.	Advisor to the Bighorn Institute, Palm Desert, CA
1984-Pres.	Member of the Technical Staff of the Desert Bighorn Council, Inc.
1992-2005	Member of the Cooperative Health and Population Study of the Peninsular bighorn sheep with CDF&G, UC Davis, and Zoological Society of San Diego.
1998-2008	Member of the Peninsular Bighorn Sheep Federal Recovery Team w/ USF&WS.
2001-2009.	Superintendent III, Anza-Borrego Desert State Park. Supervise Law Enforcement, Public Safety, Interpretation, Maintenance, and Seasonal Staff in California's largest state park.
2006-Pres.	Consultant to Ikh Nartiin Chuluu Nature Reserve, Mongolia. Assist in implementation of management plan for 110,000 acre Reserve. Help protect Argali sheep, Ibex, Cinereous Vulture, and Corsac fox. Support Sister Park agreement between Ikh Nart and Anza-Borrego Desert State Park to support operations and equipment supply. Assist in capture tagging, and banding of the Cinereous Vultures.
2008-2009	Consultant to the Abu Dhabi Authority for Cultural and Heritage. Work to assist the Emirate to develop a management plan for Jebel Hafit Nature Reserve
2009	State Park Environmental Scientist for the Colorado Desert District. Coordinate large contract for Vallecito and Carrizo watersheds. Coordinate restoration of bighorn water systems, mountain lion desert bighorn sheep research.

Certifications, Permits, Licenses, Assignments, Awards

Peace Officer Training Program, Asilomar, 1976
DPR Firearms Instructor, 1978
DPR Defensive Tactics Instructor, 1979
DPR Motorcycle Training, 1975
U.S.F.&W.S. and CDF&G Handling Permits for Least Bell's Vireo, SW Willow Flycatcher, and Desert Pupfish
Annual Herbicide Applicator's Training
Mountain Lion Handling Class, CA Dept. of Fish & Game, January 2001
P.O.S.T. and DPR Academy, Mott Training Center, November 2002
Coordinate desert bighorn annual census and participate in wildlife captures of bighorn, deer, lions.
Honorary Mayor of Borrego Springs, 2006 to 2008
Minerva Hoyt Award for 2008, Desert Conservation Award
Andrew Hill Award for Inspiration, CA State Parks Director's Award Program, 2009
Desert Protective Council Award of Merit For Desert Conservation, 2009

Personal Interests

Resource Management
Hiking
Writing and Editing
River Rafting
Hunting
Horseback Riding
Birding
Photography
Archeology
Travel

Employment Experience

2009

Retired Annuitant, Environmental Scientist

Colorado Desert District, California State Parks, Borrego Springs, CA. Coordinate contracts for resource management projects concerning bighorn sheep management, mountain lion research, and non-native tamarisk tree eradication.

2001-2009

State Park Superintendent III,

Superintendent III for California's largest state park.. Attended Mott Training Center for completion of POST law enforcement certification from May 2002 to November 2002. Oversee all sector staff and functions, including Supervising Rangers, State Park Ranger I's, Resource Ranger Team, State Park Ranger / Pilot, seasonal aids, interpreters, and maintenance personnel. Oversee $2 million budget, public outreach and educational programs, conduct and attend meetings within and outside the unit, work with media to project a professional image in the community and throughout the state. Worked 10 years with General Plan Team to produce General Plan for acceptance by the State Park Commission. Active team member on land acquisitions committee. Work Closely with Anza-Borrego Foundation and Anza-Borrego Institute. Work closely with the District Superintendent and District Specialists.

1993 to 2001

Associate State Park Resource Ecologist, Colorado Desert District. Jointly managed and implemented resource management program for seven units of California State Parks. Supervised programs and projects to restore southern California ecosystems, natural processes, and endangered species. Prepared budget requests and manage funding for annual and long-term funding programs. In 99/00 this amounted to $1.1 million in Natural Resource Deferred Maintenance and CAT I Natural Resources allocations. Supervised resource crew of one PMW I and three Park Aids. Involved in numerous wildlife capture/radio collaring projects in CA. and Sonora, Mexico involving Peninsular and Mexican bighorn sheep, mule deer, as well as the September 2001 capture of feral burros on the Lower Colorado River. Worked on the successful netgun capture of 117 feral cattle from Anza-Borrego in 1987-89. Projects conducted included Lower Colorado River riparian restoration, exotic plant removal, bighorn recovery efforts, prescribed fire in Cuyamaca, and initiation of a large-scale interagency research project to study the dynamics of cougars, mule deer, bighorn sheep and humans. Member of the Statewide Burn Team, the Anza-Borrego General Plan Team, Federal Peninsular Bighorn Recovery Team, and the Flat-Tailed Horned Lizard Interagency Coordinating Committee.

1980 to 1993

State Park Naturalist I, Anza-Borrego Desert State Park®, Colorado Desert District.Supervised all resource management projects and budgets, including supervision of up to ten seasonal employees, directing special programs in exotic plant and animal eradication, dune restoration, and habitat restoration. Prepared CEQA's. Reviewed collecting permits and publications for sale. Acted as Liaison with cooperating association for 13 years. Managed Anza-Borrego interpretive program, including scheduling of fifteen interpreters, personnel evaluations and training, brochure preparation, A-V equipment, and assisted in training corp of volunteers and volunteer naturalists. Conducted fifty interpretive programs per year throughout the park and southern California. Prepared and built 50 interpretive panels and 13 large-scale redwood and masonry park entrance signs in the field. Co-authored a large format book on Anza-Borrego, edited seven books on Anza-Borrego, and wrote numerous self-guided brochures park newspapers, as well as fifty interpretive panels located throughout the park.

Traveled to Saudi Arabia as part of a State Park System contingent to assist the Kingdom in establishment of an 80,000 acre desert park. Promoted to State Park Ranger II during my first two years as Naturalist, while on a Training and Development Assignment.

1978 to 1980

State Park Ranger I, Ocotillo Wells State Vehicular Recreation Area, (formerly a sector of Anza-Borrego). Our team developed the first Youth Certification Program for underage drivers. Enforced vehicle and park laws to insure safe operation of off-highway vehicles. Assigned as First Aid Officer, Firearms Instructor, and Defensive Tactics Instructor for OWSVRA and Anza-Borrego Desert State Park.

1976 to 1978

State Park Ranger I, Channel Coast Area. Conducted Field Training for all Trainees and Technicians in four beach units. Developed Teacher's Packet for Ventura County Schools, discovered a least tern nesting colony which subsequently was designated a State Reserve, wrote a ten part newspaper series for the 50th Anniversary of the State Park System for the Ventura Star Free Press. Worked in heavy law enforcement units to prevent auto and campsite burglaries.

1975 to 1976

State Park Ranger Trainee, San Diego Coast Area. Completed Ranger Trainee and Law Enforcement Training at Asilomar. Worked in six beach units, one State Reserve, and one Preserve. Campground duties, crime prevention, and interpretation. Represented DPR at Desert Bighorn Council meeting in Sonora, Mexico. Assisted DPR on special assignment to survey archaeological sites in the proposed Ocotillo Wells SVRA.

1974 to 1975

Contract Biologist, USDA, Inyo National Forest. Conducted study of competition between wild horses, feral burros, and bighorn sheep in the White Mountains and Inyo Mountains. Inventoried water sources and essential habitat. 80 page report to USFS. Paper presented to Desert Bighorn Council, Inc. April 1975.

1972 to 1975

Park Aid, Seasonal, Anza-Borrego Desert State Park. Researched ecology of the Peninsular bighorn sheep, including range, population dynamics, food habits, predation, water sources, and human encroachment. Forwarded recommendations to Area Manager. Winter seasons were spent as an Outpost Park Aid, patrolling and maintaining a 60,000 acre sector.

STATE OF CALIFORNIA

ENERGY RESOURCES CONSERVATION AND DEVELOPMENT COMMISSION

In the Matter of: The Application for Certification for the IVANPAH SOLAR ELECTRIC GENERATING SYSTEM	Docket No. 07-AFC-5

Testimony of Bill Powers, P.E.
Ivanpah Solar Electric Generating System
Docket 07-AFC-5

December 16, 2009

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I. Introduction

My testimony addresses the inadequate analysis of the distributed photovoltaic (PV) alternative to the proposed Ivanpah Solar Electric Generating System (ISEGS) in the Final Staff Analysis (FSA). I am a registered professional mechanical engineer in California with over 25 years of experience in the energy and environmental fields. I have permitted five 50 MW peaking turbine installations in California, as well as numerous gas turbine, microturbine, and engine cogeneration plants around the state. I organized conferences on permitting gas turbine power plants (2001) and dry cooling systems for power plants (2002) as chair of the San Diego Chapter of the Air & Waste Management Association. I am the author of the October 2007 strategic energy plan for the San Diego region titled "San Diego Smart Energy 2020." The plan uses the state's Energy Action Plan as the framework for accelerated introduction of local renewable and cogeneration distributed resources to reduce greenhouse gas emissions from power generation in the San Diego region by 50 percent by 2020. I am the author of several 2009 articles in Natural Gas & Electricity Journal on use of large-scale distributed solar photovoltaics (PV) in urban areas as a cost-effective substitute for new gas turbine peaking capacity.

II. Rooftop PV Is at the Top of the Energy Action Plan Loading Order

The FSA states, in discussing the conservation and demand-side management alternative to ISEGS, that cost-effective energy efficiency is the resource of first choice in meeting California's energy needs (p. 4-77):

> Conservation and demand-side management consist of a variety of approaches to reduction of electricity use, including energy efficiency and conservation, building and appliance standards, and load management and fuel substitution. In 2005 the Energy Commission and CPUC's Energy Action Plan II declared cost effective energy efficiency as the resource of first choice for meeting California's energy needs.

The CEC and the CPUC developed the "Energy Action Plan" in 2003 to guide strategic energy decisionmaking in California. The Energy Action Plan establishes the energy resource "loading order," or priority list that defines how California's energy needs are to be met. Energy Action Plan I was published in May 2003.[1] Energy Action Plan I describes the loading order in the following manner (p. 4):

> The Action Plan envisions a "loading order" of energy resources that will guide decisions made by the agencies jointly and singly. First, the agencies want to optimize all strategies for increasing conservation and energy efficiency to minimize increases in electricity and natural gas demand. Second, recognizing that new generation is both necessary and desirable, the agencies would like to see these needs met first by renewable energy resources and distributed generation. Third, because the preferred resources require both sufficient investment and adequate time to "get to scale," the agencies also will support additional clean, fossil fuel, central-station generation. Simultaneously, the agencies intend to improve the bulk electricity transmission grid and distribution facility infrastructure to support growing demand centers and the interconnection of new generation.

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[1] Energy Action Plan I: http://www.energy.ca.gov/energy_action_plan/2003-05-08_ACTION_PLAN.PDF

Energy Action Plan I, Under "Optimize Energy Conservation and Resource Efficiency," states (p. 5):

> Incorporate distributed generation or renewable technologies into energy efficiency standards for new building construction.

Energy Action Plan I identifies rooftop PV as a de facto energy efficiency measure with this statement. As noted in the ISEGS FSA (p. 4-77), energy efficiency is at the top of the loading order. Energy Action Plan I also states, Under "Promote Customer and Utility-Owned Distributed Generation," (p. 7):

> Distributed generation is an important local resource that can enhance reliability and provide high quality power, without compromising environmental quality. The state is promoting and encouraging clean and renewable customer and utility owned distributed generation as a key component of its energy system. Clean distributed generation should enhance the state's environmental goals. This determined and aggressive commitment to efficient, clean and renewable energy resources will provide vision and leadership to others seeking to enhance environmental quality and moderate energy sector impacts on climate change. Such resources, by their characteristics, are virtually guaranteed to serve California load. With proper inducements distributed generation will become economic.
>
> - Promote clean, small generation resources located at load centers.
> - Determine system benefits of distributed generation and related costs.
> - Develop standards so that renewable distributed generation may participate in the Renewable Portfolio Standard program.

Energy Action Plan I prioritizes rooftop PV as the preferable renewable resource, but indicates obliquely that it is costly and that in any case distributed PV is not eligible to participate in the Renewable Portfolio Standard (RPS) program. Therefore investor-owned utilities have no incentive to develop distributed PV resources. Since Energy Action Plan I was approved in 2003, PV cost has dropped dramatically. Commercial distributed PV is half the cost it was in 2003 and costs continue to drop. Residential PV is following quickly behind. Distributed PV is also now eligible for the RPS program.[2]

Energy Action Plan II was adopted in September 2005.[3] The purpose of Energy Action Plan II is stated as (p. 1): "EAP II is intended to look forward to the actions needed in California over the next few years, and to refine and strengthen the foundation prepared by EAP I." Energy Action Plan II reaffirms the loading order stating (p. 2):

> EAP II continues the strong support for the loading order – endorsed by Governor Schwarzenegger – that describes the priority sequence for actions to address increasing energy needs. The loading order identifies energy efficiency and demand response as the

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[2] CPUC Press Release – Docket A.08-03-015, *CPUC Approves Edison Solar Roof Program*, June 18, 2009. "The energy generated from the project will be used to serve Edison's retail customers and the output from these facilities will be counted towards Edison's RPS goals."

[3] Energy Action Plan II: http://www.energy.ca.gov/energy_action_plan/2005-09-21_EAP2_FINAL.PDF

> State's preferred means of meeting growing energy needs. After cost-effective efficiency and demand response, we rely on renewable sources of power and distributed generation, such as combined heat and power applications. To the extent efficiency, demand response, renewable resources, and distributed generation are unable to satisfy increasing energy and capacity needs, we support clean and efficient fossil-fired generation.

The CEC's *2009 Integrated Energy Policy Report (IEPR) – Final Committee Report* (December 2009), underscores the integration of building PV as a critical component of "net zero" energy use targets for new residential and commercial construction, under the heading "Energy Efficiency and the Environment," explaining:[4]

> With the focus on reducing GHG emissions in the electricity sector, energy efficiency takes center stage as a zero emissions strategy. One of the primary strategies to reduce GHG emissions through energy efficiency is the concept of zero net energy buildings. In the 2007 IEPR, the Energy Commission recommended increasing the efficiency standards for buildings so that, when combined with on-site generation, newly constructed buildings could be zero net energy by 2020 for residences and by 2030 for commercial buildings.
>
> A zero net energy building merges highly energy efficient building construction and state-of-the-art appliances and lighting systems to reduce a building's load and peak requirements and includes on-site renewable energy such as solar PV to meet remaining energy needs. The result is a grid-connected building that draws energy from, and feeds surplus energy to, the grid. The goal is for the building to use net zero energy over the year."

The FSA is flawed in its failure to identify rooftop PV as a higher priority in the Energy Action Plan loading order than utility-scale remote solar resources like ISEGS.

III. FSA Rationale for Eliminating Rooftop PV is Flawed

The FSA correctly describes that a distributed rooftop PV alternative has essentially no environmental impact, stating (p. 4-63 to 4-66):

- Distributed solar PV is assumed to be located on already existing structures or disturbed areas so little to no new ground disturbance would be required and there would be few associated biological impacts.
- Relatively minimal maintenance and washing of the solar panels would be required.
- Because most PV panels are black to absorb sun, rather than mirrored to reflect it, glare would not create visual impacts as with the power tower, Fresnel, and trough technologies.
- Additionally, the distributed solar PV alternative would not require the additional operational components, such as dry-cooling towers, substations, transmission interconnection, maintenance and operation facilities with corresponding visual impacts.

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[4] CEC, *2009 Integrated Energy Policy Report (IEPR) – Final Committee Report*, December 2009, p. 56.

The FSA then eliminates distributed PV, citing three specific reasons why achieving 400 MW of distributed PV is not a feasible substitute for ISEGS (FSA, p. 4-54):

- Would depend on additional policy support - Additional legislation for increased incentives may be required to achieve this level of penetration.
- Would require more PV manufacturing capacity - Building 400 MW of distributed solar PV would require an even more aggressive deployment of PV at more than double the historic rate of solar PV than the California Solar Initiative program currently employs.
- Would require PV lower cost than currently exists - systems larger than 750 kW averaged \$6.80/watt in 2007.

Each of these justifications for elimination of distributed PV is flawed, as explained in the following paragraphs.

A. Additional Policy Support is Not Required for Distributed PV to Substitute for ISEGS

ISEGS will have a capacity of 400 MW (FSA, p. 4-4). PG&E will receive 300 MW of the ISEGS output and SCE will receive 100 MW (FSA, p. 4-8). The FSA notes that more than 400 MW of distributed PV was in operation in California by the end of 2008, and the PV installation rate is increasing rapidly, nearly doubling between 2008 and 2007.

The FSA correctly describes that both SCE and PG&E, the two entities that would purchase power from the ISEGS, are constructing large distributed PV projects. The 500 MW SCE urban PV project was approved by the CPUC in June 2009. The project will be RPS-eligible and will consist of a 250 MW SCE-owned component and a 250 MW third-party component. The power purchase agreement (PPA) between ISEGS and SCE and PG&E is same type of contract mechanism that will be used by SCE to contract for the 250 MW third-party component of the SCE distributed PV project.

Progress in distributed PV installation rates under the California Solar Initiative (CSI) program provides no insight into the ability of the solar industry to carry-out multiple large-scale distributed PV projects simultaneously, in the range of 400 to 500 MW each, in California. The CSI program is not the vehicle that will be used to build these projects. These projects will be built under long-term PPAs between the distributed PV project developer and a utility within the framework of the RPS program.

An example is the PPA between PG&E and Sempra Generation for 10 MW of fixed thin-film PV in Nevada.[5] The PG&E/Sempra PPA is a technology-differentiated renewable energy contract at a price incrementally higher than the market price referent (MPR) to assure that the project developer, Sempra Generation, makes a reasonable return on its investment. The contract is in effect the equivalent of a technology differentiated feed-in tariff for solar power. No incentives beyond the federal investment tax credit and accelerated depreciation available to any solar energy project were necessary. No incentives beyond those already available would be necessary

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[5] CPUC Resolution E-4240, *Approval of a power purchase agreement (PPA) for generation from a new solar photovoltaic facility between PG&E and El Dorado Energy*, LLC (Sempra Generation), May 18, 2009.

to build 400 MW of distributed PV under long-term PPAs with PG&E and SCE to substitute for ISEGS.

Sempra Generation touts the cost of power generated by its 10 MW PV installation in Nevada as "the lowest cost solar energy in the world."[6] The company specifically mentions power tower projects (like ISEGS) as producing higher-cost solar energy and being commercially unproven, stating:[7]

> Sempra has also evaluated solar thermal power technologies, which use a field of mirrors to concentrate the sunlight to produce heat for electricity generation. The company has found that using solar panels is the cheaper option, (CEO) Allman said. He noted that some of the solar thermal power technologies, such as the use of a central tower for harvesting the heat and generating steam, have yet to be proven commercially.

SCE has a similar RPS-eligible PPA with NRG for the output of a 21 MW fixed thin-film PV array in Blythe, California.[8] This project began operation in December 2009 and also consists of fixed thin-film PV panels.

B. IOUs Need Only Provide a Basic Level of Existing Information on Individual IOU Substation Capacities to PV Developers to Interconnect Over 13,000 MW of Distributed PV with Minimal Interconnection Cost

SCE expressed confidence in its March 2008 application to the CPUC for a 250 to 500 MW urban PV project that it can absorb thousands of MW of distributed PV without additional distribution substation infrastructure, stating "SCE's Solar PV Program is targeted at the vast untapped resource of commercial and industrial rooftop space in SCE's service territory"[9] and "SCE has identified numerous potential (rooftop) leasing partners whose portfolios contain several times the amount of roof space needed for even the 500 MW program."[10]

SCE stated it has the ability to balance loads at the distribution substation level to avoid having to add additional distribution infrastructure to handle this large influx of distributed PV power.[11] SCE explains:

> SCE can coordinate the Solar PV Program with customer demand shifting using existing SCE demand reduction programs on the same circuit. This will create more fully utilized distribution circuit assets. Without such coordination, much more distribution equipment may be needed to increase solar PV deployment. SCE is uniquely situated to combine solar PV Program generation, customer demand programs, and advanced distribution circuit design

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[6] GreenTech Media, *Sempra Wants 300 MW Plus of Solar in Arizona*, April 22, 2009. "The electricity we are getting out of the 10-megawatt is the lowest cost solar energy ever generated from anywhere in the world." (CEO Michael Allman).

[7] Ibid.

[8] First Solar press release, *First Solar Sells California Solar Power Project to NRG*, November 23, 2009.

[9] SCE Application A.08-03-015, *Solar Photovoltaic (PV) Program Application*, March 27, 2008, p. 6.

[10] SCE Application A.08-03-015, *Solar Photovoltaic (PV) Program Testimony*, March 27, 2008, p. 44.

[11] SCE Application A.08-03-015, *Solar Photovoltaic (PV) Program Application*, March 27, 2008, pp. 8-9.

> and operation into one unified system. This is more cost-effective than separate and uncoordinated deployment of each element on separate circuits.[12]

As SCE states, "Because these installations will interconnect at the distribution level, they can be brought on line relatively quickly without the need to plan, permit, and construct the transmission lines."[13] This statement was repeated and expanded in the CPUC's June 18, 2009 press release regarding its approval of the 500 MW SCE urban PV project:[14]

> Added Commissioner John A. Bohn, author of the decision, "This decision is a major step forward in diversifying the mix of renewable resources in California and spurring the development of a new market niche for large scale rooftop solar applications. Unlike other generation resources, these projects can get built quickly and without the need for expensive new transmission lines. And since they are built on existing structures, these projects are extremely benign from an environmental standpoint, with neither land use, water, or air emission impacts. By authorizing both utility-owned and private development of these projects we hope to get the best from both types of ownership structures, promoting competition as well as fostering the rapid development of this nascent market."

The CPUC has also calculated, for the entire inventory of approximately 1,700 existing investor-owned utility (IOU) substations, the amount of distributed PV that could be accommodated with minimal interconnection cost based on the following reasoning:[15]

> Rule 21 specifies maximum generator size relative to the peak load on the load at the point of interconnection at 15%. So, for example, if a generator is interconnected on the low side of a distribution substation bank with a peak load of 20 MW, the maximum Rule 21 interconnection criteria would allow a 3 MW system (3 MW = 15% * 20 MW).
>
> However, the 15% criterion, which is established for all generators regardless of type, was adjusted to 30% for the purposes of determining the technical potential of PV. The 15% limit is established at a level where it is unlikely the generator would have a greater output than the load at the line segment, even in the lowest load hours in the off-peak hours and seasons (such as the middle of the night and in the spring). Since the peak output for photovoltaics is during the middle of the day, PV is unlikely to have any output when loads are lowest. Therefore, a 30% criterion was used for technical interconnection potential estimates. The discussion was held with utility distribution engineers, however, we did not consider formal engineering studies or Rule 21 committee deliberation since the purpose of the analysis was only to define potential.

The CPUC assumes that larger PV arrays will be connected directly to the substation low-side (12 kV) load bank. SDG&E estimated that the cost of a 10 MW feeder is \$0.6 million per mile.[16]

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[12] Ibid, p. 9.

[13] Ibid, p. 6.

[14] CPUC Press Release – Docket A.08-03-015, *CPUC Approves Edison Solar Roof Program*, June 18, 2009.

[15] CPUC Rulemaking R.08-08-009 – California RPS Program, Administrative Law Judge's Ruling on Additional Commission Consideration of a Feed-In Tariff, *Attachment A - Energy Division FIT Staff Proposal*, March 27, 2009, p. 15.

[16] Application No. 06-08-010, Matter of the Application of San DiegoGas & Electric Company (U-902-E) for a Certificate of Public Convenience and Necessity for the Sunrise Powerlink Transmission Project, *Chapter 5:*

The cost of a 3-mile long dedicated feeder from multiple rooftop PV arrays with a combined capacity of 10 MW to the low-side bus of the substation would be less than $2 million based on SDG&E's cost estimate.

The current capital cost for state-of-the-art commercial rooftop PV is approximately $3,700/kW$_{ac}$. The gross capital cost of 10 MW of rooftop PV at current prices would be $3,700/kW x (1,000 kW/MW) x 10 MW = $37 million. The cost to construct a dedicated feeder to interconnect 10 MW of rooftop PV would be approximately 5 percent of the gross project capital cost. This is a relatively minor cost and represents no financial impediment to developing urban rooftop PV resources.

An upgrade at the substation would be necessary to accommodate the higher powerflows in cases where distributed PV, concentrated on clusters of large rooftops, could provide up to 100 percent of a single substation's peak load. A typical 12 kV/69 kV substation can be upgraded to allow two-way powerflows for up to 100 MW of interconnected distributed PV. SDG&E estimates the cost to build a new 12 kV/69 kV substation is $25 million.[17] The upgrades necessary to allow problem-free two-way powerflow across an existing substation should cost considerably less than a new substation. However, even the cost of a new substation, at $25 million, is less than 10 percent of the gross capital cost of 100 MW of state-of-the-art PV at 2009 prices. The substation upgrade cost would be relatively minor compared to the gross capital cost of 100 MW of PV arrays, and would not present a substantive financial hurdle to developing a 100 MW distributed PV resource concentrated in an area served by a single existing substation.

As a component of the DG FIT development process, the CPUC requested data on peak loads at all IOU substations from the IOUs and compiled that information graphically as shown in Figure 1. According to the CPUC, this data was obtained from IOU distribution engineers.[18] I calculate that approximately 13,300 MW of PV can be connected directly to IOU substation load banks based on the data in Figure 1. The supporting calculations for this estimate are provided in Table 1.

The IOUs provide about two-thirds of electric power supplied in California, with publicly-owned utilities like the Los Angeles Department of Water & Power and the Sacramento Municipal Utility District and others providing the rest.[19] Assuming the substation capacity pattern in Figure 1 is also representative of the non-IOU substations, the total California-wide PV that could be interconnected at substation low-side load banks with no substantive substation upgrades would be [13,300/(2/3)] = 19,950 MW.

Prepared Rebuttal Testimony of SDG&E in Response to Phase 2 Testimony of Powers Engineering, March 28, 2008, p. 5.20.

[17] Ibid, p. 5.21.

[18] CPUC Rulemaking R.08-08-009 – California RPS Program, Administrative Law Judge's Ruling on Additional Commission Consideration of a Feed-In Tariff, *Attachment A - Energy Division FIT Staff Proposal*, March 27, 2009, pp. 15-16.

[19] CEC, *2007 Integrated Energy Policy Report*, December 2007, Figure 1-11, p. 27.

Figure 1. IOU Substation peak loads, 30% of peak load, and 10 MW reference line

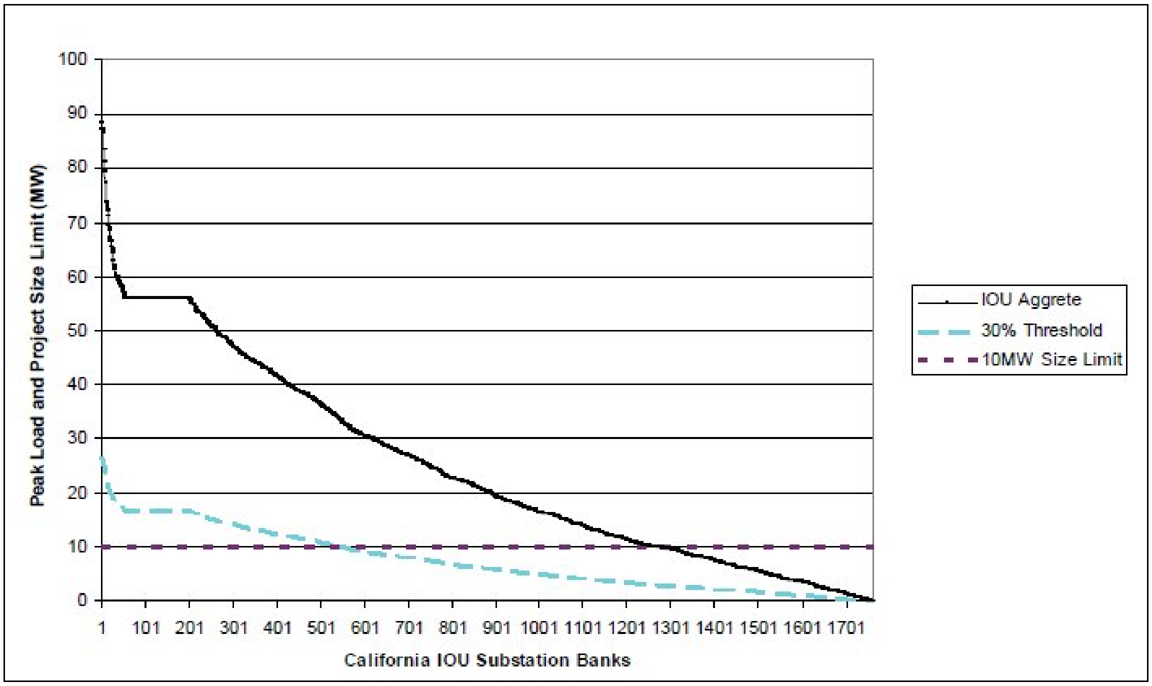

Table 1. Calculation of distributed PV interconnection capacity to existing IOU substations with minimal interconnection cost from data in Figure 1

Substation range	Number of substations	Calculation of distributed PV that could be interconnected with minimal substation upgrades (MW)	Total distributed PV potential (MW)
1-200	200	average peak ~60 MW x 0.30 = 18 MW	3,600
201-500	300	average peak ~45 MW x 0.30 = 13.5 MW	4,000
501-800	300	average peak ~30 MW x 0.30 = 9 MW	2,700
801-1,000	200	average peak ~20 MW x 0.30 = 6 MW	1,200
1,001-1,600	600	average peak ~10 MW x 0.30 = 3 MW	1,800
		Distributed PV total:	13,300

In sum, approximately 20,000 MW of distributed PV interconnection capacity is available now in California that would require little or no substation upgrading to accommodate the PV.

C. There Is No Security Justification for IOU's Withholding Information on Substation Capacities and Locations from Private PV Developers

The rationale put forth for restricting information to private distributed PV project developers includes "Providing details on distribution system could compromise homeland security" and

"Information on peak loads and system configuration may be considered commercially sensitive."[20] There is no sound basis for these two justifications.

In the first instance, climate change is seen as a major threat to national security by the U.S. defense establishment.[21] Withholding information that would allow rapid progress on addressing climate change on homeland security grounds is contrary to the national security interest. Secondly, all IOU expenditures are passed on to customers. The withholding of information on peak loads and system configuration by the IOU to protect unsubstantiated commercial sensitivity concerns, to the extent it prevents the rapid deployment of competitively-bid distributed PV in urban centers at or near the point-of-use, would have a potentially substantial negative impact on ratepayers and slow progress on addressing climate change.

Much of the necessary information is already in the public domain in some form and should be compiled and made available to distributed PV developers in a transparent and efficient format. For example, the CPUC already has the data on IOU substation interconnection limitations as shown in Figure 1. Another example is information on the location of IOU substations. Maps showing the location of all IOU substations are readily available for purchase from the CEC Cartography Unit.

The province of Ontario (Canada) makes publicly-available information on substation location and available capacity to facilitate the development of distributed PV in the province.[22] This same information protocol should be followed by California IOUs.

Finally, SCE must provide this type of information to third-party PV developers for the 250 MW private PV developer set-aside component of its 500 MW urban PV project approved by the CPUC in June 2009.

D. There is Sufficient Existing Large Commercial Roof Space in PG&E and SCE Territory to Build At Least Twenty ISEGS Plants

The 2009 IEPR Final Committee Report recognizes the huge technical potential of rooftop distributed PV to meet California's renewable energy targets, stating:[23]

> Recent studies indicate substantial technical potential for distribution-level generation resources located at or near load. A 2007 estimate from the Energy Commission suggests that there is roof space for over 60,000 MW of PV capacity, although the study did not factor in roof space that is shaded or being used for another purpose.

60,000 MW is approximately the peak summertime load for all of California, and 150 times the 400 MW capacity of ISEGS. It is important to note that the 2009 IEPR document is incorrect in asserting the 2007 rooftop PV estimate did not factor in roof shading or other limitations. The

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[20] E3 and Black & Veatch, *Straw proposal of solution to address short-term problem of information gap*, presentation at CPUC Re-DEC Working Group Meeting, December 9, 2009, p. 9. Online at: http://www.cpuc.ca.gov/PUC/energy/Renewables/Re-DEC.htm

[21] New York Times, *Climate Change Seen as Threat to U.S. Security*, August 9, 2009.

[22] E3 and Black & Veatch, *Straw proposal of solution to address short-term problem of information gap*, presentation at CPUC Re-DEC Working Group Meeting, December 9, 2009, p. 8.

[23] CEC, *2009 Integrated Energy Policy Report (IEPR) – Final Committee Report*, December 2009, p. 193.

60,000 MW estimate assumes only 24 percent of the rooftop of a typical tilt-roof residential rooftop is available for PV, and only 60 to 65 percent of flat-roof commercial rooftops are available for PV. The rationale for these estimates is explained in the 2007 (Navigant) estimate.[24]

The 60,000 MW rooftop PV estimate by Navigant does not account for any of the distributed PV described in the Renewable Energy Transmission Initiative (RETI) process. RETI is California's ongoing renewable energy transmission siting process. RETI evaluated a distributed PV alternative that would produce 27,500 MW from 20 MW increments of ground-mounted PV arrays at 1,375 non-urban substations around the state.[25] This is similar to the approach that PG&E is following. Constructing distributed PV arrays around substations is the primary focus of PG&E's 500 MW distributed PV project.[26]

Black & Veatch is the engineering contractor preparing the RETI reports. Energy & Environmental Economics, Inc. (E3) is the engineering contractor that prepared the June 2009 CPUC preliminary analysis of the cost to reach 33 percent renewable energy by 2020. These two firms now lead the CPUC's renewable distributed generation ("Re-DEC") working group process. The presentation of E3 and Black & Veatch at the December 9, 2009 initial meeting of the Re-DEC Working Group included an estimate of over 8,000 MW_{ac} of large commercial roof space in SCE and PG&E service territories in close proximity to existing distribution substations.[27]

Black & Veatch used GIS to identify large roofs in California and count available large roof area. The criteria used to select rooftops included:

- Urban areas with little available land
- Flat roofs larger than ~1/3 acre
- Assume 65 percent usable space on roof
- Within 3 miles of distribution substation

The Black & Veatch estimate for PG&E territory is 2,922 MW_{ac}. The estimate for SCE territory is 5,243 MW_{ac}. This is a combined rooftop PV capacity of over 8,000 MW_{ac}. The combined large commercial rooftop capacity is more than 20 times the 400 MW capacity of ISEGS.

Large commercial rooftop PV capacity is a subset of the universe of all commercial rooftop capacity, which includes medium and small commercial rooftops as well. A 2004 Navigant study prepared for The Energy Foundation estimated the 2010 commercial rooftop PV capacity in California at approximately 37,000 MW.[28] There is a tremendous amount of commercial roofspace available for PV. This roofspace is sufficient to fill the entire renewable energy gap necessary to reach 33 percent by 2020.

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[24] See: http://www.energy.ca.gov/2007publications/CEC-500-2007-048/CEC-500-2007-048.PDF

[25] Renewable Energy Transmission Initiative, *RETI Phase 1B Final Report*, January 2009, p. 6-25.

[26] PG&E Application A.09-02-019, *Application of Pacific Gas and Electric Company to Implement Its Photovoltaic Program*, February 24, 2009.

[27] E3 and Black & Veatch, *Summary of PV Potential Assessment in RETI and the 33% Implementation Analysis*, presentation at Re-DEC Working Group Meeting, December 9, 2009, p. 24. Online at: http://www.cpuc.ca.gov/PUC/energy/Renewables/Re-DEC.htm

[28] Navigant, *PV Grid Connected Market Potential under a Cost Breakthrough Scenario*, prepared for The Energy Foundation, September 2004, p. 83. California commercial rooftop PV potential estimated at approximately 37,000 MWp.

E. FSA Uses Unsupportable PV Cost that Is Nearly Double the Actual PV Cost in 2009

There is no justification for the FSA using obsolete CSI pricing data from 2007 to eliminate large-scale distributed PV as an alternative to ISEGS when accurate PV pricing data has been available from the SCE application for nearly two years. The FSA cites a large commercial rooftop PV cost of \$6.80/W_{ac}. All of the large commercial CSI PV installations through 2007 were conventional polycrystalline silicon PV installations. SCE provided an installed cost of \$3.50/W_{dc} (~\$4/W_{ac}) in its March 2008 application to the CPUC to build a 250 MW urban PV project. This PV project was based on using state-of-the-art thin-film PV panels, not higher-cost conventional polycrystalline silicon PV panels. As SCE stated in the application to the CPUC, "The cost to our customers of the Solar PV Program will be significant, but far less than the cost of CSI implementation."[29] SCE already had access to the 2007 CSI cost data, cited in the November 2009 FSA as a basis for eliminating the distributed PV alternative, when it made this statement in March 2008. SCE states in testimony supporting its application that "large (CSI) commercial installations cost \$6.78/W."[30] The use of obsolete and inapplicable CSI PV cost data is the only reason the FSA can erroneously assert that PV would "greatly increase the total cost of meeting state renewable energy and GHG targets."

The CPUC analyzed the cost of meeting state renewable energy requirements in June 2009.[31] Four renewable energy scenarios were analyzed: 33 percent RPS reference case, high wind case, high out-of-state delivered case, and high DG case. When current state-of-the-art PV pricing is used for high DG case, which includes a large proportion of distributed PV, the CPUC determined that there would be essentially no difference in the cost of meeting state renewable energy targets by relying predominantly on distributed PV instead of building 7,500 MW of remote solar capacity under the 33 percent RPS reference case.[32] This conclusion was reached despite a number of controversial cost assumptions by the CPUC that favored the 33 percent RPS reference case.[33]

Large-scale distributed PV has also been evaluated by RETI. The CEC is fully engaged in the RETI process. The RETI analysis of distributed PV indicates it is the least-cost solar solution to reaching California's target of 33 percent renewable energy by 2020 if state-of-the-art PV pricing is assumed. RETI makes the following points about state-of-the-art PV:[34]

> There is considerable commercial interest in utility-scale "thin film" (PV) systems. This sensitivity tests an alternate thin film technology for solar with capital costs of about \$3,700/kW_{ac}, roughly half that of tracking crystalline (PV). Notably, these (PV) capital costs are also lower than the large-scale solar thermal projects; therefore thin film solar is assumed to occur both at the distributed scale (20 MW) and also in large scale blocks (150 MW).

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[29] SCE Application A.08-03-015, *Solar Photovoltaic (PV) Program Application*, March 27, 2008, p. 7.

[30] Ibid, p. 8.

[31] CPUC, *33% Renewables Portfolio Standard Implementation Analysis Preliminary Results*, June 2009.

[32] Ibid, p. 31.

[33] RightCycle Inc. comment letter, working group member response to June 2009 *33% Renewables Portfolio Standard Implementation Analysis Preliminary Results*, in response to CPUC request for comments, August 28, 2009.

[34] California Energy Commission, *RETI Phase 1B Final Report*, January 5, 2009, p. 5-27, p. 5-28.

This August 2008 RETI report goes on to say that distributed PV at a current state-of-the-art capital cost of \$3.70/watt$_{ac}$ can provide two-thirds of what California needs going forward to reach 33 percent renewable energy by 2020:

> The results of this sensitivity run are dramatic. More importantly, the cost-competitive in-state (distributed PV resources) increase by more than 20 times to about 45,000 GWh/yr. This figure is over two-thirds of the net short requirement. The large majority of these (distributed) resources are 20 MW solar PV projects assumed to connect to the distribution system.

RETI reduced its estimate of the gap that must be filled to reach 33 percent by 2020 to 50,862 gigawatt-hours per year (GWh/yr) in October 2009.[35] RETI's estimate of 45,000 GWh/yr of cost-competitive distributed PV resources would meet approximately 90 percent of the gap of 50,862 GWh/yr identified by RETI. The CEC estimated a lower renewable energy gap of 45,000 GWh/yr in June 2009.[36]. RETI's estimate of 45,000 GWh/yr of cost-competitive distributed PV resources would meet 100 percent of the renewable energy gap identified by the CEC in June 2009.

RETI explained the genesis of the \$3.70/watt$_{ac}$ thin-film PV capital cost as:[37]

> An "alternate scenario" was proposed in the report (Section 3.8) to test lower future solar costs. Black & Veatch will run this scenario for thin film photovoltaic systems with a capital cost of \$2,700/kW$_{ac}$ to \$3,500/ kW$_{ac}$. This is based on module costs of \$1,500/ kW$_{ac}$ to \$1,700/ kW$_{ac}$ and "balance of system" costs of \$1,200/ kW$_{ac}$ to \$1,800/ kW$_{ac}$. These module costs are based on First Solar's 2010 target production cost of \$0.90/watt$_{dc}$. Balance of system includes inverters, installation, mounting systems and site costs."

First Solar states its average panel production cost in the third quarter of 2009 was \$0.85/watt$_{dc}$, somewhat less then the \$0.90/watt$_{dc}$ price basis used by Black & Veatch to establish a \$2,700/ kW$_{ac}$ to \$3,500/ kW$_{ac}$ price range for thin-film PV in the RETI process.[38] Therefore use of a \$3.70/watt$_{ac}$ capital cost is conservative for thin-film PV in 2009.

Southern California Edison's 500 MW urban warehouse PV project in San Bernardino and Riverside is based on the same PV technology (First Solar) and pricing that RETI indicates should lead to distributed PV dominating solar development in California to meet RPS goals.[39] SCE estimated a cost for its urban thin-film PV project of \$3,500/kW$_{dc}$ in its March 2008 application to the CPUC.[40] As noted, this project was approved by the CPUC in June 2009.

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[35] RETI, *Phase 2A Final Report Update – Effect of Revised Demand Forecast on RETI Net Short*, Discussion Draft, October 2009.

[36] CEC, *Impact of Assembly Bill 32 Scoping Plan Electricity Resource Goals on New Natural Gas-Fired Generation – Staff Report*, June 2009, p. 1.

[37] RETI, *Phase 1A Final Report*, August 2008, Appendix B, p. 5-5.

[38] See First Solar October 09 fact sheet: http://www.firstsolar.com/pdf/FS_Company_FastFacts_MD-5-601-NA.pdf

[39] CPUC Decision 09-06-049, June 18, 2009. See: http://docs.cpuc.ca.gov/PUBLISHED/FINAL_DECISION/102730.htm

[40] SCE Application A.08-03-015, Solar Photovoltaic (PV) Program Testimony, March 27, 2008, p. 17.

F. Market Price Referent with Adjustment for On-Peak Power Output Benefit of Distributed PV would be Sufficient Price to Assure Rapid Construction of 400 MW Distributed PV Alternative to ISEGS

The MPR that renewable energy projects are currently compared to, the cost of power generation from a hypothetical new natural gas-fired baseload power plant, is \$0.12126/kWh.[41] Solar PV produces a substantial amount of output during on-peak summer demand periods. The electric power tariff during summer on-peak periods is much higher than the average tariff over the course of a year. For example, SCE's tariff pays 3.13 times the base MPR for deliveries during the summer on-peak period.[42] SCE has determined that the adjusted MPR for a distributed PV system is 1.39 times the MPR for a baseload plant.[43] Multiplying the \$0.12126/kWh MPR by 1.39 gives an adjusted MPR of \$0.169/kWh. This price alone, based on my experience with the current pricing of distributed PV PPAs, may be a sufficient price signal for private developers to rapidly develop large-scale distributed PV in SCE and PG&E service territories.

However, the transmission & distribution benefits of distributed PV are real and have been quantified.[44] The estimated value range of the transmission and distribution benefits of distributed PV include \$0.058/kWh in SDG&E territory and \$0.023 to \$0.037/kWh in SCE territory. The transmission & distribution benefits of distributed PV in PG&E territory vary widely. Some examples in PG&E territory include Fresno at \$0.026/kWh and Stockton at \$0.039/kWh. These estimates were developed using the E3 model for calculating transmission & distribution benefits.[45]

An MPR-adjusted price of \$0.169/kWh, plus an average transmission & distribution benefit of approximately \$0.030/kWh, is equivalent to an overall value to the IOU of approximately \$0.20/kWh. Any price paid for distributed PV by an IOU below this price threshold should result in a net benefit to all of the IOU's ratepayers. A distributed PV price in the range \$0.20/kWh would be more than sufficient to create a dynamic market for third party development of large-scale distributed PV in California urban areas.

G. Retrofitting Commercial PV onto Existing Rooftops Makes It More Cost-Effective, Not Less So as Implied in the FSA

The FSA implies that retrofitting PV onto existing buildings makes rooftop PV cost-prohibitive, stating "Widespread expansion of distributed PV beyond current programs, however, would require a large number of retrofit installations. No matter how it is installed, relying heavily on PV greatly increases the total cost of meeting state renewable energy and GHG targets." This implication against retrofit PV installations is completely wrong. Commercial rooftops offer ideal platforms for large-scale PV and require minimal site preparation compared to ground-

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[41] CPUC Resolution E-4214, *2008 Market Price Referent values for use in the 2008 Renewable Portfolio Standard solicitations*, December 18, 2008. MPR, 2012 operational date, 20-yr PPA: \$0.12126/kWh.

[42] SCE Application A.08-03-015, *Solar Photovoltaic (PV) Program Supplemental Rebuttal Testimony*, October 14, 2008, p. 3, footnote 2. "ToD (time of day) adjustment estimate calculated as weighted average of (512 summer – on hours at 3.13, 768 summer – mid at 1.35, and 2,189 winter – mid hours at 1.00) = 1.39."

[43] Ibid.

[44] CPUC Rulemaking R.06-02-012, Develop Additional Methods to Implement California RPS Program, *Pre-Workshop Comments of GreenVolts, Cleantech America, and Community Environmental Council on the 2008 Market Price Referent*, March 6, 2008, p. 15.

[45] Ibid, p. 14.

mounted PV or power tower projects like ISEGS. The entire SCE urban PV project, at \$3,500/kW$_{dc}$, is based on putting PV on existing commercial rooftops. The SCE estimated labor cost of \$0.60/watt$_{dc}$ is low precisely because relatively little site preparation is required.[46]

Some utilities are already prioritizing the distributed PV alternative. The November 2008 Los Angeles Department of Water & Power "Solar Los Angeles" strategic plan is a good real-world example of this focus.[47] The plan consists of 780 megawatts of urban PV and 500 megawatts of remote solar. This is approximately 60 percent distributed PV and 40 percent remote solar. In contrast, the 33 percent RPS reference case evaluated by the CPUC, the case that assumes the renewable energy contracts signed by the IOUs proceed on schedule, includes 3,235 MW of distributed PV and 7,298 MW of remote solar thermal of all types.[48] This is approximately 30 percent distributed PV and 70 percent remote solar including ISEGS.

H. FSA Concerns about Sufficient PV Panel Manufacturing Capacity Are Baseless

The concerns expressed in the FSA regarding the availability of PV panels if 400 MW of distributed PV substitutes for ISEGS are without foundation. More than 5,000 MW of PV was installed worldwide in 2008.[49] Worldwide thin-film PV production capacity reached 3,600 MW per year in 2008. The FSA cites an incorrect and unreferenced manufacturing capacity for thin-film PV of 500 MW per year in 2008 (FSA, p. 4-66). Thin-film PV manufacturing capacity is projected to reach 7,400 MW per year in 2010. First Solar alone has manufactured and shipped more than 1,000 MW of thin-film panels to date in 2009.[50]

Worldwide conventional polycrystalline silicon PV production capacity reached 13,300 megawatts a year in 2008.[51] It is projected to reach 20,000 megawatts a year in 2010. The 2010 projections were made just as the economic slump began in late 2008. It is likely there will be some scale-back on the 2010 capacity additions due to the state of the world economy. Nonetheless, there is a tremendous amount of available worldwide PV manufacturing capacity.

PV panel manufacturing capacity has greatly expanded worldwide in the last 2 to 3 years. The current estimated oversupply of PV panel manufacturing capacity for 2010 is 8,000 MW.[52] As a result of this oversupply, the cost of conventional polycrystalline PV panels has dropped precipitously and is approaching the cost of thin-film PV panels. The *Wall Street Journal* recently reported that conventional solar panel prices have fallen by \$2 a watt since 2008, due to too much solar manufacturing capacity chasing too few solar projects.[53]

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[46] SCE Application A.08-03-015, *Solar Photovoltaic (PV) Program Testimony*, March 27, 2008, Table IV-5, p. 41. Total labor cost per 1 MW$_{dc}$ PV array estimated at \$0.61/W$_{dc}$.

[47] See: http://mayor.lacity.org/stellent/groups/electedofficials/@myr_ch_contributor/documents/contributor_web_content/lacity_004982.pdf

[48] CPUC, *33% Renewables Portfolio Standard Implementation Analysis Preliminary Results*, June 2009, p. 87.

[49] Schreiber, D. - EuPD Research, *PV Thin-film Markets, Manufacturers, Margins*, presentation at 1st Thin-Film Summit, San Francisco, December 1-2, 2008.

[50] First Solar press release, *First Solar Becomes First PV Company to Produce 1GW in a Single Year*, December 15, 2009.

[51] Schreiber, D. - EuPD Research, *PV Thin-film Markets, Manufacturers, Margins*, presentation at 1st Thin-Film Summit, San Francisco, December 1-2, 2008.

[52] B. Murphy – Fulcrum Technologies, Inc., *The Power and Potential of CdTe (thin-film) PV*, presented at 2nd Thin-Film Summit, San Francisco, December 1-2, 2009.

[53] Wall Street Journal, *Darker Times for Solar-Power Industry*, May 11, 2009.

California added 158 MW of distributed PV in 2008 (FSA, p. 4-62). California is a relatively minor player on the world PV stage. Spain added approximately 2,500 MW of primarily distributed ground-mounted PV resources in 2008.[54] Spain has a smaller economy than California. Germany, approximately the same size as California and with considerably lower solar intensity, added approximately 1,500 MW of distributed PV resources in 2008 and will add at least 2,000 MW in 2009.[55] At either of the demonstrated Spanish or German PV installation rates, California could meet its entire renewable energy gap of either 45,000 or 50,000 GWh/yr by 2020. Worldwide PV manufacturing, either thin-film alone or thin-film and conventional polycrystalline silicon, could readily supply 2,500 megawatts a year of PV demand in California now.

I. Slight Reduction in Output from Distributed PV in Los Angeles, Central Valley, or Bay Area Is Offset by Transmission Losses from ISEGS to These Load Centers

The FSA implies that the superior solar intensity at the ISEGS location in the Mojave Desert is a substantive reason for eliminating distributed PV from consideration, stating:

> The location of the distributed solar PV would impact the capacity factor of the distributed solar PV. Capacity factor depends on a number of factors including the insolation of the site. Because a distributed solar PV alternative would be located throughout the state of California, the insolation at some of these locations may be less than in the Mojave Desert.

The solar insolation at the ISEGS site is about 10 to 15 percent better than the composite solar insolation for Los Angeles, the Central Valley, and Oakland.[56,57] However, the CEC estimates average transmission losses in California at 7.5 percent and peak transmission losses at 14 percent.[58] The incrementally better solar insolation at the ISEGS site is almost completely negated by the losses incurred by transmitting ISEGS solar power to California urban areas. In contrast, distributed PV has minimal losses between generation and user.

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[54] PV Tech, *Worldwide photovoltaics installations grew 110% in 2008, says Solarbuzz*, March 16, 2009.

[55] PV Tech, *German market booming: Inverter and module supplies running out at Phoenix Solar*, November 15, 2009.

[56] U.S. DOE, *Stand-Alone Flat-plate Photovoltaic Systems: System Sizing and Life-Cycle Costing Methodology for Federal Agencies*, 1984, Appendix, p. A-27.

[57] NREL, *Solar Radiation Data Manual for Flat-Plate and Concentrating Collectors*, California cities data: http://rredc.nrel.gov/solar/pubs/redbook/PDFs/CA.PDF

[58] E-mail communication between Don Kondoleon, manager - CEC Transmission Evaluation Program, and Bill Powers of Powers Engineering, January 30, 2008.

J. CEC Has Already Determined Distributed PV Can Compete Cost-Effectively with Other Forms of Generation

The CEC denied an application for a 100-megawatt natural-gas-fired gas turbine power plant, the Chula Vista Energy Upgrade Project (CVEUP), in June 2009 in part because rooftop solar PV could potentially achieve the same objectives for comparable cost.[59]

This June 2009 CEC decision implies that any future applications for gas-fired generation in California, or any other type of generation including remote utility-scale renewable energy generation like ISEGS that require public land and new transmission to reach demand centers, should be measured against using urban PV to meet the power need. The CEC's final decision in the CVEUP case stated:[60]

> Photovoltaic arrays mounted on existing flat warehouse roofs or on top of vehicle shelters in parking lots do not consume any acreage. The warehouses and parking lots continue to perform those functions with the PV in place. (Ex. 616, p. 11.)….Mr. Powers (expert for intervenor) provided detailed analysis of the costs of such PV, concluding that there was little or no difference between the cost of energy provided by a project such as the CVEUP (gas turbine peaking plant) compared with the cost of energy provided by PV. (Ex. 616, pp. 13 – 14.)….PV does provide power at a time when demand is likely to be high—on hot, sunny days. Mr. Powers acknowledged on cross-examination that the solar peak does not match the demand peak, but testified that storage technologies exist which could be used to manage this. The essential points in Mr. Powers' testimony about the costs and practicality of PV were uncontroverted.

The CEC concluded in the CVEUP final decision that PV solar arrays on rooftops and over parking lots may be a viable alternative to the gas turbine project proposed in that case, and that if the gas turbine project proponent opted to file a new application a much more detailed analysis of the PV alternative would be required.

IV. Conclusion

The FSA analysis of the distributed PV alternative to ISEGS has many parallels to the FSA analysis of the distributed PV in the CVEUP proceeding. Flawed logic and outdated data were used to improperly eliminate distributed PV as an alternative. In fact, distributed PV is a fully viable and cost-effective alternative that eliminates the environmental impacts that would be caused by the ISEGS project. The FSA should have concluded that distributed PV is a superior alternative to the ISEGS project.

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[59] CEC, Chula Vista Energy Upgrade Project - Application for Certification (07-AFC-4) San Diego County, *Final Commission Decision*, June 2009.

[60] Ibid, pp. 29-30.

Declaration of Bill Powers, P.E.

Re: Testimony on Alternatives to the Proposed Ivanpah Solar Electric Generating System

Docket 07-AFC-5

I, Bill Powers, declare as follows:

1) I am a self-employed consulting engineer.

2) My relevant professional qualifications and experience are set forth in the attached resume and the attached testimony and are incorporated herein by reference.

3) I prepared the testimony attached hereto and incorporated herein by reference, relating to the distributed PV alternative to the project.

4) I prepared the testimony attached hereto and incorporated herein by reference relating to the proposed Project in the Ivanpah Valley in San Bernardino County.

5) It is my professional opinion that the attached testimony is true and accurate with respect to the issues that it addresses.

6) I am personally familiar with the facts and conclusions described within the attached testimony and if called as a witness, I could testify competently thereto.

I declare under penalty of perjury that the foregoing is true and correct to the best of my knowledge and belief.

Dated: Dec. 16, 2009 Signed: Bill Powers, P.E.

At: SAN DIEGO, CA

BILL POWERS, P.E.

PROFESSIONAL HISTORY

Powers Engineering, San Diego, CA 1994-
ENSR Consulting and Engineering, Camarillo, CA 1989-93
Naval Energy and Environmental Support Activity, Port Hueneme, CA 1982-87
U.S. Environmental Protection Agency, Research Triangle Park, NC 1980-81

EDUCATION

Master of Public Health – Environmental Sciences, University of North Carolina
Bachelor of Science – Mechanical Engineering, Duke University

PROFESSIONAL AFFILIATIONS

Registered Professional Mechanical Engineer, California (Certificate M24518)
American Society of Mechanical Engineers
Air & Waste Management Association

TECHNICAL SPECIALTIES

Twenty-five years of experience in:

- San Diego and Baja California regional energy planning
- Power plant technology, emissions, and cooling system assessments
- Combustion and emissions control equipment permitting, testing, monitoring
- Oil and gas technology assessment and emissions evaluation
- Latin America environmental project experience

SAN DIEGO AND BAJA CALIFORNIA REGIONAL ENERGY PLANNING

San Diego Smart Energy 2020 Plan. Author of October 2007 “San Diego Smart Energy 2020,” an energy plan that focuses on meeting the San Diego region’s electric energy needs through accelerated integration of renewable and non-renewable distributed generation, in the form of combined heat and power (CHP) systems and solar photovoltaic (PV) systems. PV would meet approximately 28 percent of the San Diego region’s electric energy demand in 2020. CHP systems would provide approximately 47 percent. Annual energy demand would drop 20 percent in 2020 relative to 2003 through use all cost-effective energy efficiency measures. This target is based on City of San Diego experience. San Diego has consistently achieved energy efficiency reductions of 20 percent on dozens of projects. Existing utility-scale gas-fired generation would continue to be utilized to provide power at night, during cloudy whether, and for grid reliability support.

Photovoltaic technology selection and siting for SDG&E Solar San Diego project. Served as PV technology expert in California Public Utilities Commission proceeding to define PV technology and sites to be used in San Diego Gas & Electric (SDG&E) $250 million “Solar San Diego” project. Recommendations included: 1) prioritize use of roof-mounted thin-film PV arrays similar to the SCE urban PV program to maximize the installed PV capacity, 2) avoid tracking ground-mounted PV arrays due to high cost and relative lack of available land in the urban/suburban core, 3) and incorporate limited storage in fixed rooftop PV arrays to maximizing output during peak demand periods. Suitable land next to SDG&E substations capable of supporting 5 to 40 MW of PV (each) was also identified by Powers Engineering as a component of this project.

Photovoltaic arrays as alternative to natural gas-fired peaking gas turbines, Chula Vista. Served as PV technology expert in California Energy Commission (CEC) proceeding regarding the application of MMC Energy to build a 100 MW peaking gas turbine power plant in Chula Vista. Presented testimony that 100 MW of PV arrays in the Chula Vista area could provide the same level of electrical reliability on hot summer days as an equivalent amount of peaking gas turbine capacity at approximately the same cost of energy. The preliminary decision issued by the presiding CEC commissioner in the case recommended denial of the application in part due to failure of the applicant or CEC staff to thoroughly evaluate the PV alternative to the proposed turbines. No final decision has yet been issued in the proceeding (as of May 2009).

San Diego Area Governments (SANDAG) Energy Working Group. Public interest representative on the SANDAG Energy Working Group (EWG). The EWG advises the Regional Planning Committee on issues related to the coordination and implementation of the Regional Energy Strategy 2030 adopted by the SANDAG Board of Directors in July 2003. The EWG consists of elected officials from the City of San Diego, County of San Diego and the four subareas of the region. In addition to elected officials, the EWG includes stakeholders representing business, energy, environment, economy, education, and consumer interests.

Development of San Diego Regional Energy Strategy 2030. Participant in the 18-month process in the 2002-2003 timeframe that led to the development of the San Diego Regional Energy Strategy 2030. This document was adopted by the SANDAG Board of Directors in July 2003 and defines strategic energy objectives for the San Diego region, including: 1) in-region power generation increase from 65% of peak demand in 2010 to 75% of peak demand in 2020, 2) 40% renewable power by 2030 with at least half of this power generated in-county, 3) reinforcement of transmission capacity as needed to achieve these objectives. The SANDAG Board of Directors voted unanimously on Nov. 17, 2006 to take no position on the Sunrise Powerlink proposal primarily because it conflicts the Regional Energy Strategy 2030 objective of increased in-region power generation. The Regional Energy Strategy 2030 is online at: http://www.energycenter.org/uploads/Regional_Energy_Strategy_Final_07_16_03.pdf

Imperial Valley Study Group. Participant in the Imperial Valley Study Group (IVSG), and effort funded by the CEC to examine transmission options for maximizing the development of geothermal resources in Imperial County. Advised the IVSG that no alternatives other than the Sunrise Powerlink or a similar variant were be considered to move Imperial Valley geothermal generation to San Diego. Initiated a dialogue on IVSG's failure to consider alternatives that was incorporated into the IVSG April 12, 2005 meeting minutes (see: http://www.energy.ca.gov/ivsg/documents/2005-04-12_meeting/2005-04-12_AMNDED_IVSG_MINUTES.PDF). Also co-authored with the Utility Consumers' Action Network an October 14, 2005 alternative letter report to the September 30, 2005 IVSG final report that documents numerous feasible transmission alternatives to the Sunrise Powerlink that were not considered by IVSG. The October 14, 2005 IVSG alternative letter report also served as a comment letter on the CEC's 2005 Integrated Energy Policy Report webpage is available at: http://www.energy.ca.gov/2005_energypolicy/documents/2005-10-11_DER_comments/10-14 05_Utility_Consumers_Action_Network_BPPWG.pdf

COMBUSTION AND EMISSIONS CONTROL EQUIPMENT PERMITTING, TESTING, MONITORING

EPRI Gas Turbine Power Plant Permitting Documents – Co-Author. Co-authored two Electric Power Research Institute (EPRI) gas turbine power plant siting documents. Responsibilities included chapter on state-of-the-art air emission control systems for simple-cycle and combined-cycle gas turbines, and authorship of sections on dry cooling and zero liquid discharge systems.

Air Permits for 50 MW Peaker Gas Turbines – Six Sites Throughout California. Responsible for preparing all aspects of air permit applications for five 50 MW FT-8 simple-cycle turbine installations at sites around California in response to emergency request by California state government for additional peaking power. Units were designed to meet 2.0 ppm NO_x using standard temperature SCR and innovative dilution air system to maintain exhaust gas temperature within acceptable SCR range. Oxidation catalyst is also used to maintain CO below 6.0 ppm.

Kauai 27 MW Cogeneration Plant – Air Emission Control System Analysis. Project manager to evaluate technical feasibility of SCR for 27 MW naphtha-fired turbine with once-through heat recovery steam generator. Permit action was stalled due to questions of SCR feasibility. Extensive analysis of the performance of existing oil-fired turbines equipped with SCR, and bench-scale tests of SCR applied to naphtha-fired turbines, indicated that SCR would perform adequately. Urea was selected as the SCR reagent given the wide availability of urea on the island. Unit is first known application of urea-injected SCR on a naphtha-fired turbine.

Microturbines – Ronald Reagan Library, Ventura County, California. Project manager and lead engineer or preparation of air permit applications for microturbines and standby boilers. The microturbines drive the heating and cooling system for the library. The microturbines are certified by the manufacturer to meet the 9 ppm NO_x emission limit for this equipment. Low-NO_x burners are BACT for the standby boilers.

Hospital Cogeneration Microturbines – South Coast Air Quality Management District. Project manager and lead engineer for preparation of air permit application for three microturbines at hospital cogeneration plant installation. The draft Authority To Construct (ATC) for this project was obtained two weeks after submittal of the ATC application. 30-day public notification was required due to the proximity of the facility to nearby schools. The final ATC was issued two months after the application was submitted, including the 30-day public notification period.

Gas Turbine Cogeneration – South Coast Air Quality Management District. Project manager and lead engineer for preparation of air permit application for two 5.5 MW gas turbines in cogeneration configuration for county government center. The turbines will be equipped with selective catalytic reduction (SCR) and oxidation catalyst to comply with SCAQMD BACT requirements. Aqueous urea will be used as the SCR reagent to avoid trigger hazardous material storage requirements. A separate permit will be obtained for the NO_x and CO continuous emissions monitoring systems. The ATCs is pending.

Industrial Boilers – NO_x BACT Evaluation for San Diego County Boilers. Project manager and lead engineer for preparation of Best Available Control Technology (BACT) evaluation for three industrial boilers to be located in San Diego County. The BACT included the review of low NO_x burners, FGR, SCR, and low temperature oxidation (LTO). State-of-the-art ultra low NO_x burners with a 9 ppm emissions guarantee were selected as NO_x BACT for these units.

Peaker Gas Turbines – Evaluation of NO_x Control Options for Installations in San Diego County. Lead engineer for evaluation of NO_x control options available for 1970s vintage simple-cycle gas turbines proposed for peaker sites in San Diego County. Dry low-NO_x (DLN) combustors, catalytic combustors, high-temperature SCR, and NO_x absorption/conversion (SCONO$_x$) were evaluated for each candidate turbine make/model. High-temperature SCR was selected as the NOx control option to meet a 5 ppm NO_x emission requirement.

Hospital Cogeneration Plant Gas Turbines – San Joaquin Valley Unified Air Pollution Control District. Project manager and lead engineer for preparation of air permit application and BACT evaluation for hospital cogeneration plant installation. The BACT included the review of DLN combustors, catalytic combustors, high-temperature SCR and SCONO$_x$. DLN combustion followed by high temperature SCR was selected as the NO_x control system for this installation. The high temperature SCR is located upstream of the heat recovery steam generator (HRSG) to allow the diversion of exhaust gas around the HRSG without compromising the effectiveness of the NO_x control system.

Industrial Cogeneration Plant Gas Turbines – Upgrade of Turbine Power Output. Project manager and lead engineer for preparation of BACT evaluation for proposed gas turbine upgrade. The BACT included the review of DLN combustors, catalytic combustors, high-, standard-, and low-temperature SCR, and SCONO$_x$. Successfully negotiated air permit that allowed facility to initially install DLN combustors and operate under a NO_x plantwide "cap." Within two major turbine overhauls, or approximately eight years, the NO_x emissions per turbine must be at or below the equivalent of 5 ppm. The 5 ppm NO_x target will be achieved through technological in-combustor NO_x control such as catalytic combustion, or SCR or SCR equivalent end-of-pipe NO_x control technologies if catalytic combustion is not available.

Gas Turbines – Modification of RATA Procedures for Time-Share CEM. Project manager and lead engineer for the development of alternate CO continuous emission monitor (CEM) Relative Accuracy Test Audit (RATA) procedures for time-share CEM system serving three 7.9 MW turbines located in San Diego. Close interaction with San Diego APCD and EPA Region 9 engineers was required to receive approval for the alternate CO RATA standard. The time-share CEM passed the subsequent annual RATA without problems as a result of changes to some of the CEM hardware and the more flexible CO RATA standard.

Gas Turbines – Evaluation of NO_x Control Technology Performance. Lead engineer for performance review of dry low-NO_x combustors, catalytic combustors, high-, standard-, and low-temperature selective catalytic reduction (SCR), and NO_x absorption/conversion ($SCONO_x$). Major turbine manufacturers and major manufacturers of end-of-pipe NO_x control systems for gas turbines were contacted to determine current cost and performance of NO_x control systems. A comparison of 1993 to 1999 "$/kwh" and "$/ton" cost of these control systems was developed in the evaluation.

Gas Turbines – Evaluation of Proposed NO_x Control System to Achieve 3 ppm Limit. Lead engineer for evaluation for proposed combined cycle gas turbine NO_x and CO control systems. Project was in litigation over contract terms, and there was concern that the GE Frame 7FA turbine could not meet the 3 ppm NO_x permit limit using a conventional combustor with water injection followed by SCR. Operations personnel at GE Frame 7FA installatins around the country were interviewed, along with principal SCR vendors, to corroborate that the installation could continuously meet the 3 ppm NO_x limit.

Gas Turbines – Title V "Presumptively Approvable" Compliance Assurance Monitoring Protocol. Project manager and lead engineer for the development of a "presumptively approval" NO_x parametric emissions monitoring system (PEMS) protocol for industrial gas turbines. "Presumptively approvable" means that any gas turbine operator selecting this monitoring protocol can presume it is acceptable to the U.S. EPA. Close interaction with the gas turbine manufacturer's design engineering staff and the U.S. EPA Emissions Measurement Branch (Research Triangle Park, NC) was required to determine modifications necessary to the current PEMS to upgrade it to "presumptively approvable" status.

Environmental Due Diligence Review of Gas Turbine Sites – Mexico. Task leader to prepare regulatory compliance due diligence review of Mexican requirements for gas turbine power plants. Project involves eleven potential sites across Mexico, three of which are under construction. Scope involves identification of all environmental, energy sales, land use, and transportation corridor requirements for power projects in Mexico. Coordinator of Mexican environmental subcontractors gathering on-site information for each site, and translator of Spanish supporting documentation to English.

Development of Air Emission Standards for Gas Turbines - Peru. Served as principal technical consultant to the Peruvian Ministry of Energy in Mines (MEM) for the development of air emission standards for Peruvian gas turbine power plants. All major gas turbine power plants in Peru are currently using water injection to increase turbine power output. Recommended that 42 ppm on natural gas and 65 ppm on diesel (corrected to 15% O_2) be established as the NO_x limit for existing gas turbine power plants. These limits reflect NO_x levels readily achievable using water injection at high load. Also recommended that new gas turbine sources be subject to a BACT review requirement.

Gas Turbines – Title V Permit Templates. Lead engineer for the development of standardized permit templates for approximately 100 gas turbines operated by the oil and gas industry in the San Joaquin Valley. Emissions limits and monitoring requirements were defined for units ranging from GE Frame 7 to Solar Saturn turbines. Stand-alone templates were developed based on turbine size and NO_x control equipment. NO_x utilized in the target turbine population ranged from water injection alone to water injection combined with SCR.

Gas Turbines – Evaluation of NO_x, SO_2 and PM Emission Profiles. Performed a comparative evaluation of the NO_x, SO_2 and particulate (PM) emission profiles of principal utility-scale gas turbines for an independent power producer evaluating project opportunities in Latin America. All gas turbine models in the 40 MW to 240 MW range manufactured by General Electric, Westinghouse, Siemens and ABB were included in the evaluation.

Stationary Internal Combustion Engine (ICE) RACT/BARCT Evaluation. Lead engineer for evaluation of retrofit NO_x control options available for the oil and gas production industry gas-fired ICE population in the San Joaquin Valley affected by proposed Best Available Retrofit Control Technology (BARCT) emission limits. Evaluation centered on lean-burn compressor engines under 500 bhp, and rich-burn constant and cyclically loaded (rod pump) engines under 200 bhp. The results of the evaluation indicated that rich burn cyclically-loaded rod pump engines comprised 50 percent of the affected ICE population, though these ICEs accounted for only 5 percent of the uncontrolled gas-fired stationary ICE NO_x emissions. Recommended retrofit NO_x control strategies included: air/fuel ratio adjustment for rod pump ICEs, Non-selective catalytic reduction (NSCR) for rich-burn, constant load ICEs, and "low emission" combustion modifications for lean burn ICEs.

Development of Air Emission Standards for Stationary ICEs - Peru. Served as principal technical consultant to the Peruvian Ministry of Energy in Mines (MEM) for the development of air emission standards for Peruvian stationary ICE power plants. Draft 1997 World Bank NO_x and particulate emission limits for stationary ICE power plants served as the basis for proposed MEM emission limits. A detailed review of ICE emissions data provided in PAMAs submitted to the MEM was performed to determine the level of effort that would be required by Peruvian industry to meet the proposed NO_x and particulate emission limits. The draft 1997 WB emission limits were revised to reflect reasonably achievable NO_x and particulate emission limits for ICEs currently in operation in Peru.

Air Toxics Testing of Natural Gas-Fired ICEs. Project manager for test plan/test program to measure volatile and semi-volatile organic air toxics compounds from fourteen gas-fired ICEs used in a variety of oil and gas production applications. Test data was utilized by oil and gas production facility owners throughout California to develop accurate ICE air toxics emission inventories.

Ethanol Plant Dryer – Penn-Mar Ethanol, LLC. Lead engineer on BACT evaluation for ethanol dryer. Dryer nitrogen oxide (NO_x) emission limit of 30 ppm determined to be BACT following exhaustive review of existing and pending ethanol plant air permits and discussions with principal dryer vendors.

BARCT Low NO_x Burner Conversion – Industrial Boilers. Lead engineer for a BARCT evaluation of low NO_x burner options for natural gas-fired industrial boilers. Also evaluated methanol and propane as stand-by fuels to replace existing diesel stand-by fuel system and replacement of steam boilers with gas turbine co-generation system.

BACT Packed Tower Scrubber/Mist Eliminator Performance Evaluations. Project manager and lead engineer for Navy-wide plating shop air pollution control technology evaluation and emissions testing program. Mist eliminators and packed tower scrubbers controlling metal plating processes, which included hard chrome, nickel, copper, cadmium and precious metals plating, were extensively tested at three Navy plating shops. Chemical cleaning and stripping tanks, including hydrochloric acid, sulfuric acid, chromic acid and caustic, were also tested. The final product of this program was a military design specification for plating and chemical cleaning shop air pollution control systems. The hydrochloric acid mist sampling procedure developed during this program received a protected patent.

BACT Packed Tower Scrubber/UV Oxidation System Pilot Test Program. Technical advisor for pilot test program of packed tower scrubber/ultraviolet (UV) light VOC oxidation system controlling VOC emissions from microchip manufacturing facility in Los Angeles. The testing was sponsored in part by the SCAQMD's Innovative Technology Demonstration Program, to demonstrate this innovative control technology as BACT for microchip manufacturing operations. The target compounds were acetone, methylethylketone (MEK) and 1,1,1-trichloroethane, and compound concentrations ranged from 10-100 ppmv. The single stage packed tower scrubber consistently achieved greater than 90% removal efficiency on the target compounds. The residence time required in the UV oxidation system for effective oxidation of the target compounds proved significantly longer than the residence time predicted by the manufacturer.

BACT Pilot Testing of Venturi Scrubber on Gas/Aerosol VOC Emission Source. Technical advisor for project to evaluate venturi scrubber as BACT for mixed phase aerosol/gaseous hydrocarbon emissions from deep fat fryer. Venturi scrubber demonstrated high removal efficiency on aerosol, low efficiency on VOC emissions. A number of VOC tests indicated negative removal efficiency. This anomaly was traced to a high hydrocarbon concentration in the scrubber water. The pilot unit had been shipped directly to the jobsite from another test location by the manufacturer without any cleaning or inspection of the pilot unit.

Pulp Mill Recovery Boiler BACT Evaluation. Lead engineer for BACT analysis for control of SO_2, NO_x, CO, TNMHC, TRS and particulate emissions from the proposed addition of a new recovery furnace at a kraft pulp mill in Washington. A "top down" approach was used to evaluate potential control technologies for each of the pollutants considered in the evaluation.

Air Pollution Control Equipment Design Specification Development. Lead engineer for the development of detailed Navy design specifications for wet scrubbers and mist eliminators. Design specifications were based on field performance evaluations conducted at the Long Beach Naval Shipyard, Norfolk Naval Shipyard, and Jacksonville Naval Air Station. This work was performed for the U.S. Navy to provide generic design specifications to assist naval facility engineering divisions with air pollution control equipment selection. Also served as project engineer for the development of Navy design specifications for ESPs and fabric filters.

POWER PLANT TECHNOLOGY, EMISSIONS, AND COOLING SYSTEM ASSESSMENTS

IGCC and Low Water Use Alternatives to Eight Pulverized Coal Fired 900 MW Boilers. Expert for cities of Houston and Dallas on integrated gasification combined cycle (IGCC) as a fully commercial coal-burning alternative to the pulverized coal (PC) technology proposed by TXU for eight 900 MW boilers in East Texas. Also analyzed East Texas as candidate location for CO_2 sequestration due to presence of mature oilfield CO_2 enhanced oil recovery opportunities and a deep saline aquifer underlying the entire region. Presented testimony on the major increase in regional consumptive water use that would be caused by the evaporative cooling towers proposed for use in the PC plants, and that consumptive water use could be lowered by using IGCC with evaporative cooling towers or by using air-cooled condensers with PC or IGCC technology. TXU ultimately dropped plans to build the eight PC plants as a condition of a corporate buy-out.

Assessment of CO_2 Capture and Sequestration for IGCC Plants. Author of assessment prepared for a public interest client of CO_2 capture and sequestration options for IGCC plants. The assessment focuses on: 1) CO_2 sequestration performance of operational large-scale CO_2 sequestration projects, specifically the Weyburn CO_2 enhanced oil recovery (EOR) project, and 2) CO_2 EOR as the vehicle to offset the cost of CO_2 capture and serve as the platform for an initial set of U.S. IGCC plants equipped for full CO_2 capture and storage.

Assessment of IGCC Alternative to Proposed 250 MW Circulating Fluidized Bed (CFB) Unit. Lead engineer to evaluate IGCC option to proposed 250 MW CFB firing Powder River Basin coal. Project site is in Montana, where CO_2 EOR opportunities exist in the eastern part of the state.

500 MW Coal-Fired Plant –Air Cooling and IGCC. Provided expert testimony on the performance of air-cooling and IGCC relative to the conventional closed-cycle wet cooled, supercritical pulverized coal boiler proposed by the applicant. Steam Pro™ coal-fired power plant design software was used to model the proposed plant and evaluate the impacts on performance of air cooling and plume-abated wet cooling. Results indicated that a conservatively designed air-cooled condenser could maintain rated power output at the design ambient temperature of 90 ^{o}F. The IGCC comparative analysis indicated that unit reliability comparable to a conventional pulverized coal unit could be achieved by including a spare gasifier in the IGCC design, and that the slightly higher capital cost of IGCC was offset by greater thermal efficiency and reduced water demand and air emissions.

Retrofit of SCR to Existing Natural Gas-Fired Units. Lead expert in successful representation of interests of the city of Carlsbad, California to prevent weakening of an existing countywide utility boiler NO_x rule. Weakening of NO_x rule would have allowed a 1,000 MW merchant utility boiler plant located in the city to operate without installing selective catalytic reduction (SCR) NO_x control systems. Ultimately the plant owner was compelled to comply with the existing NO_x rule and install SCR on all five boilers at the plant. This project required numerous appearances before the county air pollution control hearing board to successfully defend the existing utility boiler NO_x rule.

Proposed 1.500 MW Pulverized Coal Power Plant. Provided testimony challenge to air permit issued for Peabody Coal Company's proposed 1,500 MW pulverized-coal fired power plant in Kentucky. Presented case that IGCC is a superior method for producing power from coal, from both environmental and energy efficiency perspective, than the proposed pulverized-coal plant. Presented evidence that IGCC is technically feasible and cost-competitive with pulverized coal.

Presidential Permits to Two Border Power Plants – Contested Air and Water Issues. Provided testimony on the air emissions and water consumption impact of two export power plants, Intergen and Sempra, in Mexicali, Mexico, and modifications necessary to minimize these impacts, including air emission offsets and incorporation of air cooling. These two plants are located within 3 miles of the California border, are interconnected only to the SDG&E transmission grid, and under the local control of the California Independent System Operator. Provided evidence that the CAISO had restricted the amount of power these two plants could export when commercial operation began in June 2003 to avoid unacceptable levels of transmission congestion on SDG&E's transmission system. The federal judge determined that the DOE had conducted an inadequate environmental assessment before issuing the Presidential Permits for these two plants and ordered the DOE to prepare a more comprehensive assessment.

300 MW Coal-Fired Circulating Fluidized Bed Boiler Plant - Best Available NO_x Control System. Provided testimony in dispute in case where approximately 50 percent NO_x control using selective non-catalytic reduction (SNCR) was accepted as BACT for a proposed 300 MW circulating fluidized bed (CFB) boiler plant in Kentucky. Presented testimony that SNCR was capable of continuous NO_x reduction of greater than 70 percent on a CFB unit and that low-dust, hot side selective catalytic reduction (SCR) and tail-end SCR were technically feasible and could achieve greater than 90 percent NO_x reduction.

Conversion of Existing Once-Through Cooled Boilers to Wet Towers, Parallel Wet-Dry Cooling, or Dry Cooling. Prepared preliminary design for the conversion of four natural gas and/or coal-fired utility boilers (Unit 4, 235 MW; Unit 3, 135 MW; Unit 2, 65 MW; and Unit 1,65 MW) from once-through river water cooling to wet cooling towers, parallel wet-dry cooling, and dry cooling. Major design constraints were available land for location of retrofit cooling systems and need to maintain maximum steam turbine backpressure at or below 5.5 inches mercury to match performance capabilities of existing equipment. Approach temperatures of 12 ^{o}F and 13 ^{o}F were used for the wet towers. SPX Cooling Technologies F-488 plume-abated wet cells with six feet of packing were used to achieve approach temperatures of 12 ^{o}F and 13 ^{o}F. Annual energy penalty of wet tower retrofit designs is approximately 1 percent. Parallel wet-dry or dry cooling was determined to be technically feasible for Unit 3 based on straightforward access to the Unit 3 surface condenser and available land adjacent to the boiler.

Utility Boiler – Assessment of Closed-Cycle Cooling Retrofit Cost for 1,200 MW Oil-Fired Plant. Prepared an assessment of the cost and feasibility of a closed-cycle wet tower retrofit for the 1,200 MW

Roseton Generating Station in New York. Determined that the cost to retrofit the Roseton plant with plume-abated closed-cycle wet cooling was well established based on cooling tower retrofit studies performed by the original owner (Central Hudson Gas & Electric Corp.) and subsequent regulatory agency critique of the cost estimate. Also determined that elimination of redundant and/or excessive budgetary line items in owners cost estimate brings the closed-cycle retrofit in line with expected costs for comparable new or retrofit plume-abated cooling tower applications. Closed-cycle cooling has been accepted as an issue that will be adjudicated.

2,000 MW Nuclear Power Plant – Closed-Cycle Cooling Retrofit Feasibility. Prepared assessment of the cost and feasibility of a closed-cycle wet tower retrofit for the 2,000 MW Indian Point Generating Station in New York. Determined that the most appropriate arrangement for the hilly site would be an inline plume-abated wet tower instead of the round tower configuration analyzed by the owner. Use of the inline configuration would allow placement of the towers at numerous sites on the property with little or need for blasting of bedrock, greatly reducing the cost of the retrofit. Also proposed an alternative circulating cooling water piping configuration to avoid the extensive downtime projected by the owner for modifications to the existing discharge channel.

Best Available NO_x Control System for 525 MW Coal-Fired Circulating Fluidized Bed Boiler Plant. Provided testimony in dispute over whether 50 percent NO_x control using selective non-catalytic reduction (SNCR) constituted BACT for a proposed 525 MW circulating fluidized bed (CFB) boiler plant in Pennsylvania. Presented testimony that SNCR was capable of continuous NO_x reduction of greater than 70 percent on a CFB unit and that tail-end selective catalytic reduction (SCR) was technically feasible and could achieve greater than 90 percent NO_x reduction.

Evaluation of Correlation Between Opacity and PM_{10} Emissions at Coal-Fired Plant. Provided testimony on whether correlation existed between mass PM_{10} emissions and opacity during opacity excursions at large coal-fired boiler in Georgia. EPA and EPRI technical studies were reviewed to assess the correlation of opacity and mass emissions during opacity levels below and above 20 percent. A strong correlation between opacity and mass emissions was apparent at a sister plant at opacities less than 20 percent. The correlation suggests that the opacity monitor correlation underestimates mass emissions at opacities greater than 20 percent, but may continue to exhibit a good correlation for the component of mass emissions in the PM_{10} size range.

Emission Increases Associated with Retrofit of SCR Existing Coal-Fired Units. Provided testimony in successful effort to compel an existing coal-fired power plant located in Massachusetts to meet an accelerated NO_x and SO_2 emission control system retrofit schedule. Plant owner argued the installation of advanced NO_x and SO_2 control systems would generate > 1 ton/year of ancillary emissions, such as sulfuric acid mist, and that under Massachusetts Dept. of Environmental Protection regulation ancillary emissions > 1 ton/year would require a BACT evaluation and a two-year extension to retrofit schedule. Successfully demonstrated that no ancillary emissions would be generated if the retrofit NO_x and SO_2 control systems were properly sized and optimized. Plant owner committed to accelerated compliance schedule in settlement agreement.

1,000 MW Coastal Combined-Cycle Power Plant – Feasibility of Dry Cooling. Expert witness in on-going effort to require use of dry cooling on proposed 1,000 MW combined-cycle “repower” project at site of an existing 1,000 MW utility boiler plant in central coastal California. Project proponent argued that site was two small for properly sized air-cooled condenser (ACC) and that use of ACC would cause 12-month construction delay. Demonstrated that ACC could easily be located on the site by splitting total of up to 80 cells between two available locations at the site. Also demonstrated that an ACC optimized for low height and low noise would minimize or eliminate proponent claims of negative visual and noise impacts.

CONTINUOUS EMISSION MONITOR (CEM) PROJECT EXPERIENCE

Process Heater CO and NO_x CEM Relative Accuracy Testing. Project manager and lead engineer for process heater CO and NO_x analyzer relative accuracy test program at petrochemical manufacturing facility. Objective of test program was to demonstrate that performance of onsite CO and NO_x CEMs was in compliance with U.S. EPA "Boiler and Industrial Furnace" hazardous waste co-firing regulations. A TECO Model 48 CO analyzer and a TECO Model 10 NO_x analyzer were utilized during the test program to provide ±1 ppm measurement accuracy, and all test data was recorded by an automated data acquisition system. One of the two process heater CEM systems tested failed the initial test due to leaks in the gas conditioning system. Troubleshooting was performed using O_2 analyzers, and the leaking component was identified and replaced. This CEM system met all CEM relative accuracy requirements during the subsequent retest.

Performance Audit of NO_x and SO_2 CEMs at Coal-Fired Power Plant. Lead engineer on system audit and challenge gas performance audit of NO_x and SO_2 CEMs at a coal-fired power plant in southern Nevada. Dynamic and instrument calibration checks were performed on the CEMs. A detailed visual inspection of the CEM system, from the gas sampling probes at the stack to the CEM sample gas outlet tubing in the CEM trailer, was also conducted. The CEMs passed the dynamic and instrument calibration requirements specified in EPA's Performance Specification Test - 2 (NO_x and SO_2) alternative relative accuracy requirements.

AIR ENGINEERING/AIR TESTING PROJECT EXPERIENCE – GENERAL

Reverse Air Fabric Filter Retrofit Evaluation – Coal-Fired Boiler. Lead engineer for upgrade of reverse air fabric filters serving coal-fired industrial boilers. Fluorescent dye injected to pinpoint broken bags and damper leaks. Corrosion of pneumatic actuators serving reverse air valves and inadequate insulation identified as principal causes of degraded performance.

Pulse-Jet Fabric Filter Performance Evaluation – Gold Mine. Lead engineer on upgrade of pulse-jet fabric filter and associated exhaust ventilation system serving an ore-crushing facility at a gold mine. Fluorescent dye used to identify bag collar leaks, and modifications were made to pulse air cycle time and duration. This marginal source was in compliance at 20 percent of emission limit following completion of repair work.

Pulse-Jet Fabric Filter Retrofit - Gypsum Calciner. Lead engineer on upgrade of pulse-jet fabric filter controlling particulate emissions from a gypsum calciner. Recommendations included a modified bag clamping mechanism, modified hopper evacuation valve assembly, and changes to pulse air cycle time and pulse duration.

Wet Scrubber Retrofit – Plating Shop. Project engineer on retrofit evaluation of plating shop packed-bed wet scrubbers failing to meet performance guarantees during acceptance trials, due to excessive mist carryover. Recommendations included relocation of the mist eliminator (ME), substitution of the original chevron blade ME with a mesh pad ME, and use of higher density packing material to improve exhaust gas distribution. Wet scrubbers passed acceptance trials following completion of recommended modifications.

Electrostatic Precipitator (ESP) Retrofit Evaluation – MSW Boiler. Lead engineer for retrofit evaluation of single field ESP on a municipal solid waste (MSW) boiler. Recommendations included addition of automated power controller, inlet duct turning vanes, and improved collecting plate rapping system.

ESP Electric Coil Rapper Vibration Analysis Testing - Coal-Fired Boiler. Lead engineer for evaluation of ESP rapper effectiveness test program on three field ESP equipped with "magnetically induced gravity return" (MIGR) rappers. Accelerometers were placed in a grid pattern on ESP collecting plates to determine maximum instantaneous plate acceleration at a variety of rapper power setpoints. Testing showed that the rappers met performance specification requirements.

Aluminum Remelt Furnace Particulate Emissions Testing. Project manager and lead engineer for high temperature (1,600 ^oF) particulate sampling of a natural gas-fired remelt furnace at a major aluminum rolling mill. Objectives of test program were to: 1) determine if condensable particulate was present in stack gases, and 2) to validate the accuracy of the in-stack continuous opacity monitor (COM). Designed and constructed a customized high temperature (inconel) PM_{10}/Mtd 17 sampling assembly for test program. An onsite natural gas-fired boiler was also tested to provide comparative data for the condensable particulate portion of the test program. Test results showed that no significant levels of condensable particulate in the remelt furnace exhaust gas, and indicated that the remelt furnace and boiler had similar particulate emission rates. Test results also showed that the COM was accurate.

Aluminum Remelt Furnace CO and NO_x Testing. Project manager and lead engineer for continuous week-long testing of CO and NO_x emissions from aluminum remelt furnace. Objective of test program was to characterize CO and NO_x emissions from representative remelt furnace for use in the facility's criteria pollution emissions inventory. A TECO Model 48 CO analyzer and a TECO Model 10 NO_x analyzer were utilized during the test program to provide $\underline{+}1$ ppm measurement accuracy, and all test data was recorded by an automated data acquisition system.

OIL AND GAS PRODUCTION AIR ENGINEERING/TESTING EXPERIENCE

Air Toxics Testing of Oil and Gas Production Sources. Project manager and lead engineer for test plan/test program to determine VOC removal efficiency of packed tower scrubber controlling sulfur dioxide emissions from a crude oil-fired steam generator. Ratfisch 55 VOC analyzers were used to measure the packed tower scrubber VOC removal efficiency. Tedlar bag samples were collected simultaneously to correlate BTX removal efficiency to VOC removal efficiency. This test was one of hundreds of air toxics tests performed during this test program for oil and gas production facilities from 1990 to 1992. The majority of the volatile air toxics analyses were performed at in-house laboratory. Project staff developed thorough familiarity with the applications and limitations of GC/MS, GC/PID, GC/FID, GC/ECD and GC/FPD. Tedlar bags, canisters, sorbent tubes and impingers were used during sampling, along with isokinetic tests methods for multiple metals and PAHs.

Air Toxics Testing of Glycol Reboiler – Gas Processing Plant. Project manager for test program to determine emissions of BTXE from glycol reboiler vent at gas processing facility handling 12 MM/cfd of produced gas. Developed innovative test methods to accurately quantify BTXE emissions in reboiler vent gas.

Air Toxics Emissions Inventory Plan. Lead engineer for the development of generic air toxics emission estimating techniques (EETs) for oil and gas production equipment. This project was performed for the Western States Petroleum Association in response to the requirements of the California Air Toxics "Hot Spots" Act. EETs were developed for all point and fugitive oil and gas production sources of air toxics, and the specific air toxics associated with each source were identified. A pooled source emission test methodology was also developed to moderate the cost of source testing required by the Act.

Fugitive NMHC Emissions from TEOR Production Field. Project manager for the quantification of fugitive Nonmethane hydrocarbon (NMHC) emissions from a thermally enhanced oil recovery (TEOR) oil production field in Kern County, CA. This program included direct measurement of NMHC concentrations in storage tank vapor headspace and the modification of available NMHC emission factors for NMHC-emitting devices in TEOR produced gas service, such as wellheads, vapor trunklines, heat exchangers, and compressors. Modification of the existing NMHC emission factors was necessary due to the high concentration of CO_2 and water vapor in TEOR produced gases.

Fugitive Air Emissions Testing of Oil and Gas Production Fields. Project manager for test plan/test program to determine VOC and air toxics emissions from oil storage tanks, wastewater storage tanks and produced gas lines. Test results were utilized to develop comprehensive air toxics emissions inventories for oil and gas production companies participating in the test program.

Oil and Gas Production Field – Air Emissions Inventory and Air Modeling. Project manager for oil and gas production field risk assessment. Project included review and revision of the existing air toxics emission inventory, air dispersion modeling, and calculation of the acute health risk, chronic non-carcinogenic risk and carcinogenic risk of facility operations. Results indicated that fugitive H_2S emissions from facility operations posed a potential health risk at the facility fenceline.

PETROLEUM REFINERY AIR ENGINEERING/TESTING EXPERIENCE

Criteria and Air Toxic Pollutant Emissions Inventory for Proposed Refinery Modifications. Project manager and technical lead for development of baseline and future refinery air emissions inventories for process modifications required to produce oxygenated gasoline and desulfurized diesel fuel at a California refinery. State of the art criteria and air toxic pollutant emissions inventories for refinery point, fugitive and mobile sources were developed. Point source emissions estimates were generated using onsite criteria pollutant test data, onsite air toxics test data, and the latest air toxics emission factors from the statewide refinery air toxics inventory database. The fugitive volatile organic compound (VOC) emissions inventories were developed using the refinery's most recent inspection and maintenance (I&M) monitoring program test data to develop site-specific component VOC emission rates. These VOC emission rates were combined with speciated air toxics test results for the principal refinery process streams to produce fugitive VOC air toxics emission rates. The environmental impact report (EIR) that utilized this emission inventory data was the first refinery "Clean Fuels" EIR approved in California.

Air Toxic Pollutant Emissions Inventory for Existing Refinery. Project manager and technical lead for air toxic pollutant emissions inventory at major California refinery. Emission factors were developed for refinery heaters, boilers, flares, sulfur recovery units, coker deheading, IC engines, storage tanks, process fugitives, and catalyst regeneration units. Onsite source test results were utilized to characterize emissions from refinery combustion devices. Where representative source test results were not available, AP-42 VOC emission factors were combined with available VOC air toxics speciation profiles to estimate VOC air toxic emission rates. A risk assessment based on this emissions inventory indicated a relatively low health risk associated with refinery operations. Benzene, 1,3-butadiene and PAHs were the principal health risk related pollutants emitted.

Air Toxics Testing of Refinery Combustion Sources. Project manager for comprehensive air toxics testing program at a major California refinery. Metals, Cr^{+6}, PAHs, H_2S and speciated VOC emissions were measured from refinery combustion sources. High temperature Cr^{+6} stack testing using the EPA Cr^{+6} test method was performed for the first time in California during this test program. Representatives from the California Air Resources Board source test team performed simultaneous testing using ARB Method 425 (Cr^{+6}) to compare the results of EPA and ARB Cr^{+6} test methodologies. The ARB approved the test results generated using the high temperature EPA Cr^{+6} test method.

Air Toxics Testing of Refinery Fugitive Sources. Project manager for test program to characterize air toxic fugitive VOC emissions from fifteen distinct process units at major California refinery. Gas, light liquid, and heavy liquid process streams were sampled. BTXE, 1,3-butadiene and propylene concentrations were quantified in gas samples, while BTXE, cresol and phenol concentrations were measured in liquid samples. Test results were combined with AP-42 fugitive VOC emission factors for valves, fittings, compressors, pumps and PRVs to calculate fugitive air toxics VOC emission rates.

LATIN AMERICA ENVIRONMENTAL PROJECT EXPERIENCE

Preliminary Design of Ambient Air Quality Monitoring Network – Lima, Peru. Project leader for project to prepare specifications for a fourteen station ambient air quality monitoring network for the municipality of Lima, Peru. Network includes four complete gaseous pollutant, particulate, and meteorological parameter monitoring stations, as well as eight PM_{10} and TSP monitoring stations.

Evaluation of Proposed Ambient Air Quality Network Modernization Project – Venezuela. Analyzed a plan to modernize and expand the ambient air monitoring network in Venezuela. Project was performed for the U.S. Trade and Development Agency. Direct interaction with policy makers at the Ministerio del Ambiente y de los Recursos Naturales Renovables (MARNR) in Caracas was a major component of this project.

Evaluation of U.S.-Mexico Border Region Copper Smelter Compliance with Treaty Obligations – Mexico. Project manager and lead engineer to evaluate compliance of U.S. and Mexican border region copper smelters with the SO_2 monitoring, recordkeeping and reporting requirements in Annex IV [Copper Smelters] of the La Paz Environmental Treaty. Identified potential problems with current ambient and stack monitoring practices that could result in underestimating the impact of SO_2 emissions from some of these copper smelters. Identified additional source types, including hazardous waste incinerators and power plants, that should be considered for inclusion in the La Paz Treaty process.

Development of Air Emission Standards for Petroleum Refinery Equipment - Peru. Served as principal technical consultant to the Peruvian Ministry of Energy in Mines (MEM) for the development of air emission standards for Peruvian petroleum refineries. The sources included in the scope of this project included: 1) SO_2 and NO_x refinery heaters and boilers, 2) desulfurization of crude oil, particulate and SO_2 controls for fluid catalytic cracking units (FCCU), 3) VOC and CO emissions from flares, 4) vapor recovery systems for marine unloading, truck loading, and crude oil/refined products storage tanks, and 5) VOC emissions from process fugitive sources such as pressure relief valves, pumps, compressors and flanges. Proposed emission limits were developed for new and existing refineries based on a thorough evaluation of the available air emission control technologies for the affected refinery sources. Leading vendors of refinery control technology, such as John Zink and Exxon Research, provided estimates of retrofit costs for the largest Peruvian refinery, La Pampilla, located in Lima. Meetings were held in Lima with refinery operators and MEM staff to discuss the proposed emission limits and incorporate mutually agreed upon revisions to the proposed limits for existing Peruvian refineries.

Development of Air Emission Limits for ICE Cogeneration Plant - Panamá. Lead engineer assisting U.S. cogeneration plant developer to permit an ICE cogeneration plant at a hotel/casino complex in Panama. Recommended the use of modified draft World Bank NO_x and PM limits for ICE power plants. The modification consisted of adding a thermal efficiency factor adjustment to the draft World Bank NO_x and PM limits. These proposed ICE emission limits are currently being reviewed by Panamanian environmental authorities.

Mercury Emissions Inventory for Stationary Sources in Northern Mexico. Project manager and lead engineer to estimate mercury emissions from stationary sources in Northern Mexico. Major potential sources of mercury emissions include solid- and liquid-fueled power plants, cement kilns co-firing hazardous waste, and non-ferrous metal smelters. Emission estimates were provided for approximately eighty of these sources located in Northern Mexico. Coordinated efforts of two Mexican subcontractors, located in Mexico City and Hermosillo, to obtain process throughput data for each source included in the inventory.

Translation of U.S. EPA Scrap Tire Combustion Emissions Estimation Document – Mexico. Evaluated the Translated a U.S. EPA scrap tire combustion emissions estimation document from English to Spanish for use by Latin American environmental professionals.

Environmental Audit of Aluminum Production Facilities – Venezuela. Evaluated the capabilities of existing air, wastewater and solid/hazardous waste control systems used by the aluminum industry in eastern Venezuela. This industry will be privatized in the near future. Estimated the cost to bring these control systems into compliance with air, wastewater and solid/hazardous waste standards recently promulgated in Venezuela. Also served as technical translator for team of U.S. environmental engineers involved in the due diligence assessment.

Assessment of Environmental Improvement Projects – Chile and Peru. Evaluated potential air, water, soil remediation and waste recycling projects in Lima, Peru and Santiago, Chile for feasibility study funding by the U.S. Trade and Development Agency. Project required onsite interaction with in-country decisionmakers (in Spanish). Projects recommended for feasibility study funding included: 1) an air quality technical support project for the Santiago, Chile region, and 2) soil remediation/metals recovery projects at two copper mine/smelter sites in Peru.

Air Pollution Control Training Course – Mexico. Conducted two-day Spanish language air quality training course for environmental managers of assembly plants in Mexicali, Mexico. Spanish-language course manual prepared by Powers Engineering. Practical laboratory included training in use of combustion gas analyzer, flame ionization detector (FID), photoionization detector (PID), and occupational sampling.

Renewable Energy Resource Assessment Proposal – Panama. Translated and managed winning bid to evaluate wind energy potential in Panama. Direct interaction with the director of development at the national utility monopoly (IRHE) was a key component of this project.

Comprehensive Air Emissions Testing at Assembly Plant – Mexico. Project manager and field supervisor of emissions testing for particulates, NO_x, SO_2 and CO at turbocharger/air cooler assembly plant in Mexicali, Mexico. Source specific emission rates were developed for each point source at the facility during the test program. Translated test report into Spanish for review by the Mexican federal environmental agency (SEMARNAP).

Air Pollution Control Equipment Retrofit Evaluation – Mexico. Project manager and lead engineer for comprehensive evaluation of air pollution control equipment and industrial ventilation systems in use at assembly plant consisting of four major facilities. Equipment evaluated included fabric filters controlling blast booth emissions, electrostatic precipitator controlling welding fumes, and industrial ventilation systems controlling welding fumes, chemical cleaning tank emissions, and hot combustion gas emissions. Recommendations included modifications to fabric filter cleaning cycle, preventative maintenance program for the electrostatic precipitator, and redesign of the industrial ventilation system exhaust hoods to improve capture efficiency.

Comprehensive Air Emissions Testing at Assembly Plant – Mexico. Project manager and field supervisor of emissions testing for particulates, NO_x, SO_2 and CO at automotive components assembly plant in Acuña, Mexico. Source-specific emission rates were developed for each point source at the facility during the test program. Translated test report into Spanish.

Fluent in Spanish. Studied at the Universidad de Michoacán in Morelia, Mexico, 1993, and at the Colegio de España in Salamanca, Spain, 1987-88. Have lectured (in Spanish) on air monitoring and control equipment at the Instituto Tecnológico de Tijuana. Maintain contact with Comisión Federal de Electricidad engineers responsible for operation of wind and geothermal power plants in Mexico, and am comfortable operating in the Mexican business environment.

PUBLICATIONS

Bill Powers, "*San Diego Smart Energy 2020 – The 21st Century Alternative*," San Diego, October 2007.

Bill Powers, "*Energy, the Environment, and the California – Baja California Border Region*," Electricity Journal, Vol. 18, Issue 6, July 2005, pp. 77-84.

W.E. Powers, *"Peak and Annual Average Energy Efficiency Penalty of Optimized Air-Cooled Condenser on 515 MW Fossil Fuel-Fired Utility Boiler,"* presented at California Energy Commission/Electric Power Research Institute Advanced Cooling Technologies Symposium, Sacramento, California, June 2005.

W.E. Powers, R. Wydrum, P. Morris, *"Design and Performance of Optimized Air-Cooled Condenser at Crockett Cogeneration Plant,"* presented at EPA Symposium on Technologies for Protecting Aquatic Organisms from Cooling Water Intake Structures, Washington, DC, May 2003.

P. Pai, D. Niemi, W.E. Powers, *"A North American Anthropogenic Inventory of Mercury Emissions,"* to be presented at Air & Waste Management Association Annual Conference in Salt Lake City, UT, June 2000.

P.J. Blau and W.E. Powers, *"Control of Hazardous Air Emissions from Secondary Aluminum Casting Furnace Operations Through a Combination of: Upstream Pollution Prevention Measures, Process Modifications and End-of-Pipe Controls,"* presented at 1997 AWMA/EPA Emerging Solutions to VOC & Air Toxics Control Conference, San Diego, CA, February 1997.

W.E. Powers, et. al., *"Hazardous Air Pollutant Emission Inventory for Stationary Sources in Nogales, Sonora, Mexico ,"* presented at 1995 AWMA/EPA Emissions Inventory Specialty Conference, RTP, NC, October 1995.

W.E. Powers, *"Develop of a Parametric Emissions Monitoring System to Predict NO_x Emissions from Industrial Gas Turbines,"* presented at 1995 AWMA Golden West Chapter Air Pollution Control Specialty Conference, Ventura, California, March 1995.

W. E. Powers, et. al., *"Retrofit Control Options for Particulate Emissions from Magnesium Sulfite Recovery Boilers,"* presented at 1992 TAPPI Envr. Conference, April 1992. Published in *TAPPI Journal*, July 1992.

S. S. Parmar, M. Short, W. E. Powers, *"Determination of Total Gaseous Hydrocarbon Emissions from an Aluminum Rolling Mill Using Methods 25, 25A, and an Oxidation Technique,"* presented at U.S. EPA Measurement of Toxic and Related Air Pollutants Conference, May 1992.

N. Meeks, W. E. Powers, *"Air Toxics Emissions from Gas-Fired Internal Combustion Engines,"* presented at AIChE Summer Meeting, August 1990.

W. E. Powers, *"Air Pollution Control of Plating Shop Processes,"* presented at 7th AES/EPA Conference on Pollution Control in the Electroplating Industry, January 1986. Published in *Plating and Surface Finishing* magazine, July 1986.

H. M. Davenport, W. E. Powers, *"Affect of Low Cost Modifications on the Performance of an Undersized Electrostatic Precipitator,"* presented at 79th Air Pollution Control Association Conference, June 1986.

AWARDS

Engineer of the Year, 1991 – ENSR Consulting and Engineering, Camarillo
Engineer of the Year, 1986 – Naval Energy and Environmental Support Activity, Port Hueneme
Productivity Excellence Award, 1985 – U. S. Department of Defense

PATENTS

Sedimentation Chamber for Sizing Acid Mist, Navy Case Number 70094

STATE OF CALIFORNIA

Energy Resources Conservation and Development Commission

In the Matter of: APPLICATION FOR CERTIFICATION FOR THE IVANPAH SOLAR ELECTRIC GENERATING SYSTEM	DOCKET NO. 07-AFC-5

INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY

Testimony of Ileene Anderson

Re: Impacts to Sensitive Wildlife from the Proposed Ivanpah Solar Electric Generating System

Docket 07-AFC-5

Summary of Testimony

The proposed project will be detrimental to numerous rare species. In some instances the FSA fails to even identify impacts. Elsewhere, the FSA fails to adequately avoid, minimize and mitigate the impacts to these rare species as required under CEQA (and NEPA).

The proposed project in itself as well as in conjunction with other cumulative and connected projects will further imperil already rare species driving them closer to extinction and will result in the need for additional species to be safeguarded under Endangered Species Act protection.

Qualifications

My qualifications are provided on my Resume attached to this Testimony and as discussed below.

I have over 20 years of experience in identifying, surveying for and documenting biological resources in southern California, including the Mojave desert.

I have a Master's of Science in Biology and a Bachelor's of Arts in Biology from the California State University, Northridge. I have continuing education in restoration/revegetation/reclamation of native habitats at the University of California, Riverside.

I have directed and participated in numerous field surveys for federal- and state-listed threatened and endangered species, as well as other rare and common species. I have written results in conformance with the California Environmental Quality Act and the National Environmental Policy Act.

I have written, implemented and monitored a variety of restoration and revegetation plans, primarily implemented as mitigation.

I have published articles on these subjects in peer-reviewed scientific journals and presented papers/posters at scientific meetings.

I have provided expert testimony on plant and animal issues at State Water Resources Control Board and California Public Utilities Commission hearings.

I was a two-term federal appointee to the BLM's California Desert Advisory Council representing renewable resources, and served one year as chairperson.

I am currently a staff biologist with the Center for Biological Diversity, where I focus on native natural resource issues primarily in southern California, including desert regions of San Bernardino County.

Statement

After my review of the biological sections of the FSA, I agree that the project as proposed would have major impacts to the biological resources of the Ivanpah Valley, affecting many sensitive plant and wildlife species and eliminating a broad expanse of relatively undisturbed Mojave Desert habitat (FSA at 6.2-95). However, my conclusion is that the FSA does not comprehensively assess the impacts from of the proposed project on the biological resources as thoroughly as is needed to inform decision makers about the comprehensive impacts of the project. Typically a project of this size would involve many seasons of surveys to thoroughly document all of the resources that occur on the site. This is particularly important in the desert regions because of the unpredictable and variable precipitation patterns. Failure to conduct sufficient surveys prior to construction of the project also effectively eliminates the most important function of surveys - using the information from the surveys to minimize harm caused by the project and reduce the need for mitigation. Often efforts to mitigate harm are far less effective than preventing the harm in the first place. In addition, without understanding the scope of harm before it occurs, it is difficult to quantify an appropriate amount and type of mitigation.

Wildlife

Birds

The FSA recognizes the potential impact to diurnal birds from flying into the focused sun rays and getting burned (FSA at pg. 6.2-65). However the FSA fails to address the additional fatalities that have been documented to occur from birds running into mirrors (McCrary 1986). Adjacent to the proposed project site is the golf course, which includes several water features. This adjacent land use attracts migratory and resident birds based on the resources present – an oasis in the desert. The FSA does not quantify the number of birds (rare or otherwise) that use/traverse the project site (mean daily count). Nor does it evaluate the impact to birds based on the McCrary (1986) results, which estimated 1.7 birds deaths per week on a 32 ha site with one 86 m tower. The proposed project site is approximately 1644 ha (over 50 times larger) with seven 95m towers and five 140 m towers. Lacking baseline data of mean daily count on the project site, analysis of the impacts to birds is impossible, and the impact maybe significant.

Migratory birds were noted to occur on the proposed site (FSA at pg. 6.2-15). Clearly the site is within a migratory pathway and the migratory elevation is a key issue that needs further analysis. Mirrors and towers within migratory elevations will create impacts to migratory birds. These impacts could be avoided or minimized if mirrors and towers are properly cited. CEQA requires that impacts be avoided and minimized.

These analyses needed to be done prior to the FSA/DEIS being produced and still need to be done, because detailed surveys and analyses are the basis for the evaluation of impacts to biological resources as required by CEQA (and NEPA). Including basic surveys and analyses in the FSA/DEIS is necessary if the public is to have an opportunity to comment on measures to avoid, minimize and then mitigate the effects of the project.

Golden eagle

Golden eagles are documented to use proposed project site as a foraging (FSA at 6.2-22) and are thought to nest in the adjacent Clark Mountains (FSA at 6.2-23). The proposed mitigation measure BIO-17proposes to reduce impacts to the species to less than significant levels, however the FSA fails to present exactly how it will mitigate the loss of the substantial amount of foraging habitat for the golden eagle. The fact still remains that significant amounts of foraging habitat will decrease carrying capacity of the landscape and could result in a potential loss of habitat needed to support a nesting pair. Because the golden eagle is a “fully protected” species under the California Endangered Species Act, the FSA fails to address this “take” issue. The individual birds may fly elsewhere, but the conversion of habitat to industrial development eliminates the ability of the eagles to use the area, forcing them into other eagles’ already occupied ranges resulting in a cumulative lethal “take” for the species.

The FSA fails to disclose even generally the location of the golden eagle nest in the Clark Mountains. Scientific literature on this subject is clear - the presence of humans detected by a raptor in its nesting or hunting habitat can be a significant habitat-altering disturbance even if the human is far from an active nest (Richardson and Miller 1997). Regardless of distance, a straightline view of disturbance affects raptors, and an effective approach to mitigate impacts of disturbance for golden eagles involved calculation of viewsheds using a three-dimensional GIS tool and development of buffers based on this (Camp et al. 1997; Richardson and Miller 1997). The FSA fails to discuss the potential impacts on nesting golden eagles in the Clark Mountains which is part of the Mojave National Preserve.

The FSA does not actually clearly analyze the impacts to and mitigations for the golden eagle under the Bald Eagle and Golden Eagle Protection Act.

Banded Gila Monster

Mitigation measure “Bio-11” for the banded Gila monster proposes relocation as the strategy if the lizard is encountered. Relocation of banded Gila monster has been shown to be an ineffective strategy (Sullivan et al. 2004). Similar to desert tortoises, the Gila monsters try to return to their original sites despite relocation distances. Effective mitigation for this species needs to include strategies that will minimize mortality, not ensure it.

American badger

Badgers were identified in the project area during surveys in 2007 (FSA at pg. 6.2-45). The territory of badgers supported in the literature indicates that badger home territories range from 340 to 1,230 hectares (Long 1973, Goodrich and Buskirk 1998). Therefore, the proposed project could displace *at least* one badger from the site. While surveys prior to construction are clearly essential since badgers have been located on the site, relocation of badgers into suitable habitat may result in introducing them into existing badger’s territory. Studies need to be provided on badger territories if animals are to be relocated in order to increase chances of persistence and suitable habitat should be identified.

Insects

While I am unaware of any scientific literature that quantitatively documents the impact of concentrated solar facilities on insects, anecdotal information from my discussions with a biological surveyor on the Daggett Solar 1 site indicate that diurnal insects including butterflies were impacted from the focused sunlight. The FSA completely fails to identify this issue. The FSA does note that many of the sensitive bird species are insectivores and rely on ample amounts of insects in their diet. Additionally, many of the resident plant species including rare plants rely on insects for pollination. Clearly the impacts to insects will need to be analyzed in the FSA including the effects on the secondary consumers (birds) and plants.

Habitat Loss and Compensatory Mitigation

For many of the rare wildlife species, "Bio-17" is proposed as the mitigation for impacts. "Bio-17" is focused on compensatory mitigation for desert tortoise through the acquisition and conservation of *at least* 8,146 acres, which I support. However, the mitigation measure needs to require that the mitigation actually benefit the other rare animals – just as it states for state jurisdictional water, where at least 198 acres of waters must be acquired. Rare or imperiled species that rely on "Bio-17" for mitigation include the American badger, banded Gila monster, burrowing owl, golden eagle, loggerhead shrike, Brewer's sparrow, crissal thrasher, and Le Conte's thrasher. In order to truly offset impacts to these rare species, the compensatory mitigation must require that acquired lands actually contain habitat for these species and that they are actually located on the mitigation lands, which will require surveys. The FSA needs to clarify if the BLM desert tortoise mitigation will also be used for compensatory land purchase by the California Department of Fish and Game (as per their comment letter 2009-10-27_CDFG_PSA_Comments_TN 53837) or if it will be used for some other form of mitigation.

Even with rare species occurring on the mitigation lands, the FSA must still recognize that the proposed project is a net loss of occupied habitat and possibly individuals of these species.

Closure, Revegetation and Rehabilitation Plan

Desert lands are notoriously hard to revegetate or rehabilitate (Lovich and Bainbridge 1999) and revegetation never supports the same diversity that originally occurred in the plant community prior to disturbance (Longcore 1997). The task of revegetating over six square miles will be a Herculean effort that will require significant financial resources. In order to assure that the ambitious goals of this revegetation effort is met post project closure, it will be necessary to bond the project, so that all revegetation obligations will met and assured. The bond needs to be structured so that it is tied to meeting the specific revegetation criteria.

The species list for the project site shows much greater diversity than the twelve species identified as Seeds Targeted for Collection in Support of Revegetation (Table 7.1 at pg. 7-10 of the Closure, Revegetation and Rehabilitation Plan). The seed list needs to be greatly increased to capture the original diversity of both perennial and annual species.

Enabling an accelerated successional process is appropriate and desirable, however, the plan should not rely on dispersal of late successional propagules over the six square mile area, but should instead include sequential seeding, where later successional species are introduced by seed after early successional species establishment. This strategy would encourage quicker re-establishment of late successional species throughout the site.

Revegetation Criteria

I unequivocally support revegetation criteria in general as a method for assessing success of revegetation efforts, and the revegetation criteria (Table 7-6 at pg. 7-32 of the Closure, Revegetation and Rehabiliation Plan) are a good start to assessing the success of the proposed revegetation effort. One important absent component is the annual flora. Admittedly tricky to monitor but essential to the landscape level integrity of the revegetated area, revegetation criteria need to be developed and included for the annual flora, based on trends in the cover and diversity of species over the 10 year monitoring period.

Because the actual proposed project site data revealed an elevational cline in shrub cover, density and richness (greater cover, density and richness at higher elevations than lower), the revegetation criteria needs to also reflect that elevational effect.

Clarifications should also be made in the revegetation criteria to preclude future interpretations that the percent cover is the *total cover* of the perennial species on the ground (as opposed to a percent of the original cover) and the same concept must be clarified with the species diversity and richness.

Fire Threats

Fire in desert ecosystems is well documented to cause catastrophic landscape scale changes (Brown and Minnich 1986, Lovich and Bainbridge 1999, Brooks 2000, Brooks and Draper 2006, Brooks and Minnich 2007) and impacts to the local species (Ducher 2009). While the FSA mentions the impacts of fire via the proliferation of non-native weeds (FSA at pg. 6.2-34 and pg. 6.2-63), it fails to adequately analyze the impacts of this issue for this proposed project that routinely relies on superheated liquids. It fails to adequately analyze the impact that a fire could have on the natural lands adjacent to the project site if it escaped from the site or address the mitigation of this impact. Instead it defers it to the Worker Environmental Awareness Program (WEAP) and only requires “a discussion of fire prevention measures to be implemented by workers during project activities” (FSA at pg. 6.2-102). A fire prevention and protection plan needs to be required to preclude the escape of fire onto the adjacent landscape (avoidance), lay out clear guidelines for protocols if the fire does spread to adjacent wildlands (minimization) and a revegetation plan if fire does occur on adjacent lands originating from the project site (mitigation) or caused by any activities associated with construction or operation of the site even if the fire originates off of the project site..

Impacts to National Park Service Lands and Resources

As mentioned above with regards to golden eagles, no analysis is presented on how the proposed project is likely to affect the wildlife and resources on the adjacent Mojave National Preserve including bighorn sheep populations as well as many other species.

Conclusions

I would like to summarize my conclusions as follows:

There is a paucity of analysis or mitigation for many of the rare wildlife species. I find the review of impacts and suggested mitigations to be unsatisfactory. Without this basic information about the use of the area by a variety of wildlife it is impossible to assess the extent of the impacts to species n population in this area from the proposed project.

The documents seem to indicate that the staff believes that all the potential wildlife impacts can be resolved by simply purchasing land elsewhere suitable for the desert tortoise. While desert tortoise habitat acquisition and protection in other areas is an essential keystone of mitigation for the loss of habitat at the proposed project site, it does not and cannot mitigate for the loss of habitat of other species if their habitat does not occur on the compensation lands.

I suggest that the missing field studies be conducted by knowledgeable researchers on the project site to fill in the missing data gaps which are the basis for analyzing impacts. Absent any real information in the field, any suggested mitigation or perceived impacts are pure conjecture. I also suggest that field studies be initiated on any proposed compensation lands to assure that proper habitat is acquired to help mitigate impacts.

The revegatation criteria need to include the important annual plant component and must be tied to the bond. More diversity in the seed mix and sequential seeding needs to be incorporated.

In summary, I find the document to be sorely lacking as it pertains to wildlife resources. These deficiencies need to be addressed and remedied before in the FSA prior to project permitting. If the project is approved despite the lack of information on many impacts, a robust monitoring and reporting system should be implemented in order to assess impacts to wildlife and other biological resources.

Declaration of Ileene E. Anderson

Re: Impacts to Wildlife and Plants from the Proposed Ivanpah Solar Electric Generating System

Docket 07-AFC-5

I, Ileene Anderson, declare as follows:

1) I am currently a biologist for the Center for Biological Diversity. I have worked with the organization for five years.

2) My relevant professional qualifications and experience are set forth in the attached resume and the attached testimony and are incorporated herein by reference.

3) I prepared the testimony attached hereto and incorporated herein by reference, relating to the impacts of the Project on wildlife and plants.

4) I prepared the testimony attached hereto and incorporated herein by reference relating to the proposed Project in the Ivanpah Valley in San Bernardino County.

5) It is my professional opinion that the attached testimony is true and accurate with respect to the issues that is addressed.

6) I am personally familiar with the facts and conclusions described within the attached testimony and if called as a witness, I could testify competently thereto.

I declare under penalty of perjury that the foregoing is true and correct to the best of my knowledge and belief.

Dated: 12/17/09 Signed:

At: Los Angeles, California

Curriculum Vitae
For
Ileene Anderson

Education

- M.S. with Distinction, Biology, California State University, Northridge, 1992
- B.A. Cum Laude, Biology, California State University, Northridge, 1989
- A.S. with Honors, Electronics, Bakersfield College, 1981

Professional Experience

2005 – present

Biologist and Public Lands Desert Director with the non-profit Center for Biological Diversity. Provide scientific expertise necessary for the conservation of California's internationally recognized unique flora and fauna in a variety of public and private land use arenas. My primary projects focus on central and southern California, including the California deserts, Tejon Ranch, Santa Ana River issues, Santa Clara River issues and numerous projects that occur within their watersheds. I comment on California Environmental Quality Act and/or National Environmental Policy Act, write petitions for plant and animal protection under the federal and state Endangered Species Act, provide scientific expertise for lawsuit settlement agreements, do public/media relations, and organize volunteers for a variety of conservation issues.

1997- 2005

Southern California Regional Botanist for the non-profit California Native Plant Society (CNPS). Provided scientific expertise necessary for the conservation of California's unique vegetation types in a variety of public and private land use plans, including the Four Southern California Forests Updated Land Use Management Plan, the West Mojave Habitat Conservation Plan, the West Riverside Multiple Species Habitat Conservation Plan, the Northern and Eastern Colorado Desert Plan, the Northern and Eastern Mojave Desert Plan, and many other smaller planning efforts. I have commented on hundreds of California Environmental Quality Act and/or National Environmental Policy Act documents, written petitions for plant protection under the federal Endangered Species Act, provided scientific expertise for lawsuit settlement agreements, done public relations in both print and radio, ran CNPS internal consensus building meetings, and organized volunteers for a variety of conservation and fund-raising issues.

1995 – 2005

Consultant on a variety of botanical projects, including rare plant surveys, quantitative and qualitative vegetation community characterization, restoration plans, vegetation monitoring and weed surveys. Project locations comprise a variety of plant communities in southern/central California including riparian, coastal sage scrub, alluvial fan scrub, alkali meadows, chaparral, and a variety of desert scrubs. A full list of projects is available upon request.

1996 – 1999

Part-time instructor at College of the Canyons (community college in Valencia, California). Courses included Introductory Biology for majors (Organismal/Environmental and Cellular/Molecular), Current Topics in Environmental Biology, and Botany. I also developed a course in Economic Botany.

1992 – 1995

Lead Botanist for The Chambers Group (an environmental consulting firm). Projects for which I was responsible included mapping, inventories, and rare plant surveys, which were written in compliance with NEPA and/or CEQA guidelines, including impact analysis and mitigation. This information was typically included in Biological Assessments (BAs), Environmental Assessments (EAs), Environmental Impact Reports (EIRs) or Environmental Impact Statements (EISs). Supervisory duties included coordinating two other botanists. Project management was also part of my duties.

1990 – 1994

Sales Associate at the Theodore Payne Foundation. This part-time job primarily included helping customers select appropriate native plant material for their gardens. Other duties included propagation and transplantation of native plant species.

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1990-1992

Herbarium Curatorial Assistant at Rancho Santa Ana Botanic Gardens. Herbarium specimen mounting and curation from international collections was the primary responsibility.

Professional Courses/Seminars

Methods of Habitat Restoration - University of California, Riverside, Winter 1993
Desert Restoration - SERCAL, October 1993
Habitat Restoration Evaluation - University of California, Riverside, Winter 1994
Basic Wetlands Delineation - Wetland Training Institute, Inc. November 1995
Mycorrhizae in Habitat Restoration - University of California, Riverside, Winter 1995
Soils Workshop – Natural Resources Conservation Service, November 1998
Plant Community Characterization and Series Identification– Native Plant Society, June 1999
Statistical Analysis for the Modified Whittaker Plot – Colorado State University, August 2002

Professional Affiliations

BLM California Desert Advisory Council - Appointee Representing Renewable Resources (Chairperson 2001) from 1996-2002
California Botanical Society
California Native Plant Society – Conservation Committee; Legal Committee.
Friends of the Santa Clara River – Director at Large
Rancho Santa Ana Botanic Gardens – Research Associate.
Society for Ecological Restoration – Coastal Sage Scrub Guild Co-coordinator (1995-2001)
Southern California Botanists – Director at Large (1994-2002)

Expert Witness

State Water Resources Control Board – May 2007 – Testified on Santa Ana River plant and animal issues
California Public Utilities Commission – March 2008 – Testified on plant issues for Sunrise Powerlink Project.

Publications and Posters

Dickey, John, Maurice Hall, Mark Madison, Jason Smesrud, Margot Griswold, Quitterie Cotten, Mica Heilmann, Greg Roland, Jim Jordahl, Richard Harasick, Wayne Bamossy, Richard Coles, Lizanne Wheeler, Pat Brown, Kevin Burton, Rick Fornelli, Ileene Anderson, Melissa Riedel-Lehrke, Ron Tiller, and Jim Richards 2005. Managing salt to stabilize the Owens Playa with saltgrass. Presented at the Center for Water Resources, Salinity Conference, Sacramento California.

Rodgers, Jane and Ileene Anderson 2002. A Rare Mint (Monardella robisonii) in a Rock-Climbing Mecca. Joshua Tree National Park. April 2002. Pgs 25 + appendices.

Anderson, Ileene, Margot Griswold, Dana Kamada, and Adrian Wolf. 2001. Coyote Canyon Landfill: Native Vegetation Restoration Results in Habitat Creation for a Threatened Species. Poster given at Society for Conservation Biology. July 2001.

Hartman, Steve and Ileene Anderson 1999. California Deserts in Transition: Ecosystem Planning. Fremontia 27(2): 13-17.

Anderson, Ileene 1998. Status of Sensitive Plant Populations on Public Grazing Allotments within the California Desert Conservation Area. California Native Plant Society. August 1998 Pgs. 34.

Recommendations for protecting raptors from human disturbance: a review

Cary T. Richardson and Clinton K. Miller

In a survey of resource managers, LeFranc and Millsap (1984) identified human-associated disturbance as a primary threat to raptor populations. Several studies have demonstrated declines in raptor populations resulting from human-associated disturbance (Voous 1977, Swenson 1979, Craighead and Mindell 1981). Resource managers can successfully use spatial and temporal buffer zones in concert to protect raptors from the effects of recreational activity (Swenson 1979, Knight and Skagen 1988, Holmes et al. 1993), human development (Ramakka and Woyewodzic 1993), and oil development (Squires et al. 1993). Spatial and temporal restrictions (buffer zones) are useful tools for resource managers to protect raptors during periods of extreme sensitivity (Knight and Skagen 1988, Knight and Temple 1995). We present information relevant to the establishment of buffer zones and the guidelines for assessing spatial and temporal buffer zones for a variety of raptors in North America. This review may serve as a general guideline for resource managers and others interested in protecting raptors.

The need for nest site protection

Human activities are known to impact raptors in at least 3 ways: (1) by physically harming or killing eggs, young, or adults; (2) by altering habitats; and (3) by disrupting normal behavior (Postovit and Postovit 1987). Due to the broad range of direct and indirect human-associated impacts and the fluctuating levels of sensitivity for individual raptors, depending on life stage and time of year, buffer zones are most effective when spatial and temporal restrictions are congruent.

The direct effects of human disturbance may seem inconsequential to uninformed or unconcerned outdoor recreationists. Activities like rock-climbing, can have severe impacts on nesting raptors, even when climbers do not have direct contact with eggs, young, or adults (Lanier and Joseph 1989, Kelly 1996). This sport often involves shouting and other noises which are disturbing enough to raptors to keep them away from their nests (Call 1979, Ratcliffe 1980). Even brief absence by parent birds can lead to missed feedings, predation on eggs or young, or to overheating, chilling, or desiccation of eggs or young (Call 1979, Suter and Joness 1981). Rock-climbing near peregrine falcon (*Falco peregrinus*) eyries during the nesting season can cause nest abandonment; some peregrine falcons are extremely sensitive and refuse to breed if humans have been in the vicinity of their eyries (Snow 1972, Olsen and Olsen 1980). Ferruginous hawks (*Buteo regalis*) tend to desert their nests if adults are exposed to human activity during incubation (White and Thurow 1985). Van Daele and Van Daele (1982) found that incubation at successful osprey (*Pandion haliaetus*) nests occurred durring 99.5-100% of daylight hours. Human disturbance during the critical periods of incubation and the early nesting stages can be fatal to embryos and nestlings.

The presence of humans detected by a raptor in its nesting or hunting habitat can be a significant habitat-altering disturbance even if the human is far from an active nest. Impacts of human activities on wild animals are often reduced when animals are shielded visually from such activities (Postovit and Postovit 1987, Knight and Temple 1995). A clear line of sight is an important factor in a raptor's response to a par-

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Key words: buffer zones, closures, conservation management, flushing distance, human disturbance, raptor

ticular disturbance (Suter and Joness 1981). A Geographic Information System-assisted viewshed approach combined with a designated buffer zone distance was found to be an effective tool for reducing potential disturbance to golden eagles (*Aquila chrysaetos*) in Northern Colorado (R. L. Knight, Colo. State Univ., Fort Collins, pers. commun.).

Human disturbance was listed as the cause of 85% of all known nest losses occurring during Boeker and Ray's (1971) study of golden eagles. Disturbance of wintering bald eagles (*Haliaeetus leucocephalus*) resulted in both increased energy expenditures due to avoidance flights and decreased energy intake due to interference with feeding activities (Stalmaster 1983). The enforcement of spatial and temporal buffer zones can protect raptors from the effects of visual disturbances (e.g., human development or recreation), audible disturbances, and direct disturbances (e.g., shooting, recreational rock-climbing).

Determining adequate protection

Several authors have provided general recommendations for determining adequate site-specific buffer zones (Postovit and Postovit 1987, Pomerantz et al. 1988, Holmes et al. 1993). Postovit and Postovit (1987) detailed steps for mitigation planning. Pomerantz et al. (1988) gave a useful set of guidelines that could be used to determine the compatibility of recreational activities in sensitive resource areas. In designing appropriate buffer zones the most important factors are: site-specific information on the horizontal and vertical proximity of a nest to a potential disturbance, source or duration of disturbance, and disturbance history of the individual raptors (Suter and Joness 1981, Postovit and Postovit 1987, Knight and Skagen 1988, Holmes et al. 1993).

Site-specific information

Physical characteristics (i.e., topography, vegetation) are important variables to consider when establishing buffer zones based on raptors' visual-and auditory-detection distances. Horizontal spatial restrictions can be shortened or lengthened depending on the height of perching or nesting sites (Holmes et al. 1993). Given variable nesting phenology of different species and regional climatic variation, exact dates of nest-site closures should be modified according to local situations (U.S. Fish and Wildl. Serv. 1984). White and Thurow (1985) recommend that the degree to which a nest is exposed or concealed should be considered when designing buffers for ferruginous hawks. They also suggested that information on the general health and status of individual populations be considered. For example, in years of food scarcity, spatial buffers should be expanded substantially.

Source or type of disturbance

Management plans should be tailored to each species, habitat, season, and source of disturbance. For example, Holmes et al. (1993) argued that, because humans in vehicles are less disruptive to raptors than pedestrians, management plans should offer different restrictions based on disturbance type. Squires et al. (1993) suggested that prairie falcons (*Falco mexicanus*) could cope with limited development on their foraging areas if their nest sites were secure from direct human disturbance. Nonthreatening activities, such as those occurring on recreational trails, may be compatible with a nest or perch location in close proximity if that activity is visually or audially buffered by vegetation or topography (Knight and Temple 1995).

Prior disturbance history of individual raptors

Due to variation of tolerance between bald eagle populations, Stalmaster and Newman (1978) suggested monitoring adult behavior prior to the establishment of management recommendations and buffer zones to determine to what extent the individuals had been sensitized to human disturbance. They noted that although a single direct disturbance may have insignificant impacts, repeated direct disturbances may cause abandonment of a nest or perch location.

Spatial and temporal buffer recommendations

Spatial buffers

Spatial buffer-zone recommendations depend on site specific considerations, and vary considerably for species such as osprey, Cooper's hawk (*Accipiter cooperii*), northern goshawk (*Accipiter gentilis*), sharp-shinned hawk (*Accipiter striatus*), golden eagle, red-tailed hawk, (*Buteo jamaicensis*), ferruginous hawk, bald eagle, prairie falcon, peregrine falcon, and American kestrel (*Falco sparverius*; Table 1). Median distances recommended for buffer zones for nesting raptors (based on the information summarized in Table 1) are as follows: osprey = 1,000 m (range = 400-1,500 m, n = 3), Cooper's hawk = 525 m (range = 400-600 m, n = 2), northern goshawk = 450 m (n = 1), sharp-shinned hawk = 450 m (n = 1), golden eagle = 800 m (range = 200-1,600 m, n = 3),

Table 1. Summary of recommendations for spatial and temporal buffer-zones for nesting raptors.

Species	Spatial (m)	Temporal	Reason for closure	Source
osprey	1,500	not discussed	human activity	Van Daele and Van Daele 1982
	400	Apr 1–Aug 31	no explanation	Colo. Div. Wildl. 1995
	1,000	during incubation	recreational disturbance	Swenson 1979
Cooper's hawk	600	not specified	habitat alteration	Bosakowski et al. 1993
	400–500	not specified	unspecified disturbance	Jones 1979
northern goshawk	400–500	not specified	unspecified disturbance	Jones 1979
sharp-shinned hawk	400–500	not specified	unspecified disturbance	Jones 1979
golden eagle	200 from cliff tops; 400 from base	Mar 1–Jun 30	human disturbance	M. Ball, U.S. For. Serv., Fort Collins, Colo., pers. commun.
	800	Feb 1–Aug 1	noise	Call 1979
	200–1,600	Mar 1–Sep 1	visual, audible	Suter and Joness 1981
	800	Feb 1–Jul 15	no explanation	Colo. Div. Wildl. 1995
red-tailed hawk	800	Feb 1–Aug 1	noise	Call 1979
ferruginous hawk	200–800	arrival–post fledging	visual, audible	Suter and Joness 1981
	250	during incubation	human activity	White and Thurow 1985
	800	Feb 1–Jul 15	no explanation	Colo. Div. Wildl. 1995
bald eagle	400	Feb 1–Aug 15	human disturbance	D. Flath, Mont. Dep. Fish, Wildl. & Parks, Bozeman, pers. commun.
	800	Feb 1–Aug 1	noise	Call 1979
	500	not discussed	human disturbance	Fraser 1983
	250	prior to egg laying through incubation	human activity	Grier et al. 1983
	800	Nov 15–Jul 31	no explanation	Colo. Div. Wildl. 1995
prairie falcon	200 from cliff tops; 400 from base	Mar 1–Jun 30	human disturbance	M. Ball, U.S. For. Serv., Fort Collins, Colo., pers. commun.
	800	Feb 1–Aug 1	noise	Call 1979
	200–800	arrival-post fledging	visual, audible	Suter and Joness 1981
	800	Mar 15–Jul 31	no explanation	Colo. Div. Wildl. 1995
	50	Mar 15–post fledging	visual	Natl. Park Serv. 1995
peregrine falcon	800	Feb 1–Jul 15	climbing disturbance	S. Johnson, Natl. Park Serv., pers. commun.
	800–1,500	not discussed	recreational disturbance	Windsor 1975
	800	Feb. 1–Aug. 1	noise	Call 1979
	1,600	Feb 1–Aug 31	human activity	U.S. Fish and Wildl. Serv. 1984
	800	Mar 15–Jul 31	no explanation	Colo. Div. Wildl. 1995
American kestrel	200 from cliff tops; 400 from base	Mar 1–Jun 30	human disturbance	M. Ball, U.S. For. Serv., Fort Collins, Colo., pers. commun.
	50	Mar 15–post-fledging	visual	Natl. Park Serv. 1995

red-tailed hawk = 800 m ($n = 1$), ferruginous hawk = 500 m (range = 200-800 m, $n = 3$), bald eagle = 500 m (range = 250-800 m, $n = 5$), prairie falcon = 650 m (range = 50-800 m, $n = 4$), peregrine falcon = 800 m (range = 800-1,600 m, $n = 5$), and American kestrel = 50-200 m ($n = 2$). Several studies have recorded flushing distances for raptors resonding to disturbances from pedestrians and vehicles (Table 2).

Table 2. Flushing distances (m) for raptors in response to disturbance by pedestrians and vehicles.

Species	Pedestrian disturbance	Vehicle disturbance	Source
golden eagle	105–390	14–190	Holmes et al. 1993
ferruginous hawk	13–165	110–280	Holmes et al. 1993
	136.4 (range = 29–291)	117.2 (range = 24–316)	White and Thurow 1985
rough-legged hawk	55–900	9–170	Holmes et al. 1993
bald eagle	50–990	50–990	Fraser 1983
	57–991 (91% > 200 m)	not studied	Fraser et al. 1985
prairie falcon	24–185	18–200	Holmes et al. 1993
American kestrel	10–100	12–115	Holmes et al. 1993
merlin	17–180	44–85	Holmes et al. 1993

Temporal buffers

For temporal restrictions to be effective, they must be tailored to individual populations. In addition, temporal restrictions need only be in effect when raptors are using a critical resource such as a nest site or foraging area (Knight and Skagen 1988). Temporal buffers should encompass all nesting activities and extend at least from the arrival of the adult birds in the nesting area through the first few weeks of nestling development (Fyfe and Olendorff 1976, Suter and Joness 1981, Grier et al. 1983, White and Thurow 1985). Adult birds often sit tightly on eggs or young nestlings, and when adults flush abruptly due to disturbances, there is increased liklihood of their ejecting the contents of their nests (Grier and Fyfe 1987).

Summary

Several studies have documented flushing distance responses of raptors to a variety of activities during breeding and nonbreeding seasons (Table 2); however, except for anecdotal and incidental reports, few studies have experimentally documented disturbance distances for use in buffer-zone recommendations (White and Thurow 1985, Holmes et al. 1993). The wide range of recommendations (Table 1) probably reflects site-specific anthropogenic and environmental conditions (Suter and Joness 1981, Fraser 1983). To be effective, buffer zones should be based on empirical evidence of wildlife responses to disturbance (Knight and Skagen 1988). Several authors suggest the need for further disturbance studies to determine flushing responses among different species (White and Thurow 1985, Postovit and Postovit 1987, Knight and Temple 1995).

The City of Boulder Open Space Department and Mountain Parks Division have used spatial and temporal buffer zones successfully for a number of years to protect cliff-nesting peregrine falcons, prairie falcons, and golden eagles. Closures are in effect from February through July annually and vary in distance by 50-400 m depending on topography, nest location, and species. Extensive public education accompanies the closures, including direct mailings to outdoor recreation shops in the area, closure signs at trailheads, press releases, and access to a 24-hour telephone information line and a site on the World Wide Web. In addition, nest sites are monitored weekly by trained volunteers. With proper planning, extensive observations of target individuals and groups, and aggressive public education, spatial and temporal buffer zones provide a useful tool for protecting raptors to resource managers.

Acknowledgments. We thank R. Moraga for his insightful comments in the development of this manuscript, S. Susnowitz for her invaluable editing, D. Packard for taking the time to review this manuscript, and L. Clauge for her assistance with formatting. The following people were very helpful and responded to phone interviews and requests for unpublished information: R. Knight, M. Ball, G. Beatty, G. Craig, D. Flath, B. Pedigue, J. Freilich, F. Howe, S. Johnson, W. Keck, S. Muehlhauser, T. Rash, B. Rogers, R. Seavers, and S. Williams.

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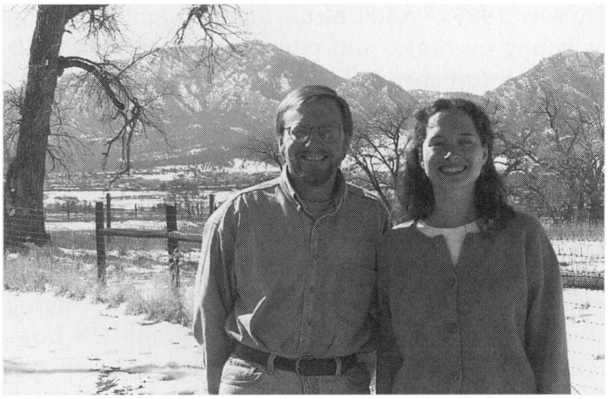

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In press, *2nd Interface Between Ecology and Land Development in California*
J.E. Keeley, Coordinator. Occidental College, April 18-19, 1997.

On the Perils of Ecological Restoration: Lessons from the El Segundo Blue Butterfly

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Abstract . Land use planning and permitting in southern California increasingly relies on ecological restoration as mitigation for damage done to natural habitats by development projects. Many restoration attempts fail miserably, for a number of reasons. Three areas of concern for restoration projects are: 1) historical accuracy and completeness, 2) ecotype accuracy, and 3) type conversions. Using evidence from a restoration project for the El Segundo blue butterfly we will show the importance of historical accuracy in ecological restoration. Other examples from the El Segundo dunes will illustrate the vital importance of using local ecotypes in restoration projects. Finally, we will discuss the issues raised by type conversions and other questionable restoration practices, why they are allowed as mitigation, and their effect on regional conservation goals.

Keywords : Restoration; mitigation; historical accuracy; ecotype accuracy; type conversion; El Segundo blue butterfly

INTRODUCTION

Ecological restoration is used as a mitigation for damage done to natural habitats and species by development projects. Although such restoration projects take place under the auspices of public agencies such as the U.S. Army Corps of Engineers, the U.S. Fish and Wildlife Service, the California Coastal Commission, and the California Department of Fish and Game, they often are plagued by weaknesses that go largely unnoticed or unquestioned by environmental activists, the academic community, politicians, and the agencies themselves. Drawing from experience with a revegetation project for the El Segundo blue butterfly, we explore some of the common pitfalls of restoration projects.

Any discussion of restoration requires an understanding of what is meant by the word. The definition arrived upon by a National Research Council committee was "the return of an ecosystem to a close approximation of its condition prior to disturbance" (NRC 1992). Unfortunately, mitigation almost never has recreation of the historic conditions as its goal, rather, success is defined as establishment of the dominant vegetation in an area (unpublished data and California Ecological Restoration Projects Inventory 1997). If historic conditions are not the goal, as they rarely are, the question arises whether restoration is undertaken to reassemble the species and ecotypes historically present or to use different species that the restorationist believes will serve the same function in the ecosystem. The distinction here is made between a concentration on *diversity* or *function.* Jordan *et al.* (1987) suggest that restorationists can illustrate their understanding of ecosystems by *imitating* rather than *copying* natural systems. They claim that insight from restoration research will be gained from being able to "create communities that resemble other communities in various ways, but that actually *differ* from them in species composition" (Jordan *et al.* 1987: 17). We differ from Jordan *et al.* about the goals of restoration and restoration research. For reasons that will be illustrated below, we believe that restoration should have as its goal the preservation of biodiversity in a system that requires minimal human management and that is historically accurate and historically complete. To qualify as a "restoration" a project should strive to be historically complete and accurate and consider the reintroduction or management of all biodiversity, including insects, mammals, birds, plants, and cryptobiotic crusts. A project that reintroduces the historically present plants is a "revegetation," a project that only establishes the dominant cover is a "partial revegetation," and any project that establishes species not native to the site is an exercise in "landscaping."

A second aspect of the definition of restoration is what has been called "the ecotype question" (Cairns 1987: 316, Kline and Howell 1987: 84). Debate centers around the relative importance of matching local ecotypes when reestablishing plants on a restoration site. Although academic consensus seems to support using local ecotypes (see Millar and Libby 1989, Read *et al.* 1996, Allen 1997), we illustrate the importance of local ecotypes on higher trophic levels and the maintenance of biodiversity. A project that does not use local ecotypes is not a "restoration."

The final facet of restoration that we discuss is whether type conversion — the creation of one natu-

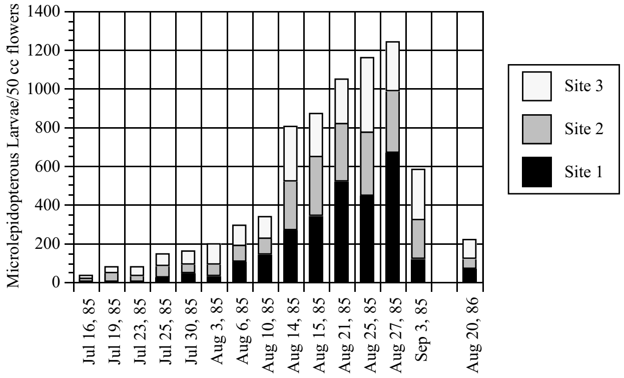

Fig. 1. Abundance of larval microlepidopterous competitors of the ESB (Gelechiidae and Cochylidae) on *Eriogonum parvifolium* at three sites at LAX (Pratt 1987).

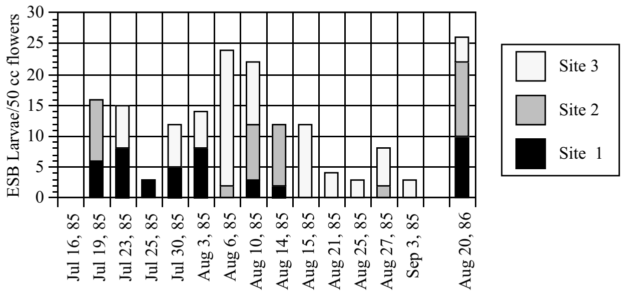

Fig. 2. Abundance of ESB larvae on *Eriogonum parvifolium* at three sites at LAX (Pratt 1987).

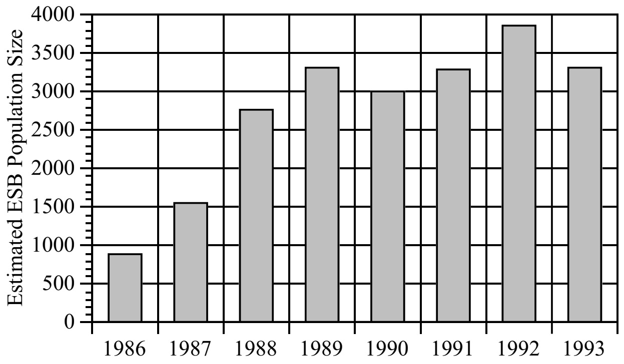

Fig. 3. Recovery of ESB population following removal of *Eriogonum fasciculatum* and provision of more foodplant (Mattoni *et al.,* in prep.).

ral community in an area that was previously occupied by another natural community — constitutes restoration. Examples of this specific kind of historical inaccuracy abound, especially for wetland and riparian restoration projects (Allen and Feddema 1996). We argue that ecological restoration does not include type conversions.

HISTORICAL ACCURACY AND COMPLETENESS

A story illustrates the dangers of historical inaccuracy. The El Segundo blue butterfly (*Euphilotes bernardino allyni* Shields) (ESB) was distributed historically along the El Segundo dunes from Ballona Creek to the Palos Verdes Peninsula (Mattoni 1992). Its sole foodplant for all life stages is the coastal buckwheat, *Eriogonum parvifolium* Smith. Larvae feed on the flowerheads, pupate directly beneath the plant, and adults perch, mate, usually nectar, lay eggs, and probably die on flowerheads (Mattoni 1992).

The ESB persists in greatest numbers on the dunes at the Los Angeles International Airport (LAX). In 1975 the backdune at LAX was recontoured to realign Pershing Drive. The recontoured backdunes were stabilized with a "natural" seed mix (Mattoni 1989a). Although perhaps well intentioned, the seed mix was representative of coastal sage scrub, not the native dune scrub community. Whether this effort was meant as a restoration is irrelevant, the event of interest is that common buckwheat (*Eriogonum fasciculatum* (Benth.) Torrey & A. Gray) was introduced and established on the dunes.[1]

Numerous other insects exploit *Eriogonum* flowerheads, which results in intense competition for the resource. This guild of competitors includes at least ten species of Lepidoptera in addition to an unknown number of other orders. While the ESB is univoltine (one generation per year) and is specialized for the short, late blooming season of *E. parvifolium*, other competitors are more opportunistic and will utilize multiple hosts. The introduction of the earlier blooming *E. fasciculatum* to the dunes therefore had the result of differentially increasing populations of competitors by providing another food source that the ESB could not exploit. Pratt (1987) showed that there was a doubling of competitive larvae on *E. parvifolium* flowerheads in mid-August, which, considering an average generation time of one month, corresponded with senescence of *E. fasciculatum* in mid-July. Increased concentrations of other larvae correlated with depressed ESB populations. Experiments confirmed that other microlepidopterous larvae outcompete and even cannibalize ESB larvae. In addition, the other moths probably provide a reserve of parasitoids that they share with the ESB (Pratt 1987, Mattoni 1988). The increase in ESB and decrease in other larvae shown in the 1986 follow-up sample is likely the result of intense pruning of *E. fasciculatum* to delay flowering.

Mattoni initiated a revegetation program on the LAX dunes in 1986; one of the first actions was the removal of *E. fasciculatum* (Mattoni 1989b). Recovery

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[1] Also present in the seed mix were *Coreopsis gigantea* (Kellogg) H.M. Hall, *Atriplex canescens* (Pursh) Nutt., *Lupinus excubitus* M.E. Jones, *Eriogonum giganteum* S. Watson, *E. cinereum* Benth., and other nonnative species. Only *E. fasciculatum* has expanded on the dunes; the others are gradually disappearing.

of the ESB over the course of the revegetation program is estimated by using a model based on transect counts (Mattoni *et al.*, in prep.). Increases in the first two years of the program can largely be attributed to removal of *E. fasciculatum*, because newly established *E. parvifolium* had not yet matured. The resonating effect of *E. fasciculatum* on insect community composition shows the result of introducing just one species that is not native to an area. This observation implies that attention paid to historical distribution of species is a crucial first step to ensure the ecological integrity of restoration projects.

Another implication of this example, gained from recognizing the far-reaching effects of just one species on natural community composition, is that restoration should also strive to be historically complete. Although moths and butterflies are rarely target species for restoration projects, and almost never considered in mitigation design, many depend on a single host plant species. Furthermore, butterflies often depend on the rare species in a community, which are often overlooked in restoration efforts. The notion of the importance of a single species on the ecosystem is not new; Paine's (1969) metaphor of the "keystone species" was intended, in his words, "to convey a sense of nature's dynamic fragility and the unsuspected consequences of removing (or adding) species" (Paine 1995). *Omission of one plant species can result in a significantly impoverished restoration.*

A second motivation for historical completeness in restoration projects is that speciose systems are more stable with respect to environmental factors (Putnam 1994:145–147). Walker has termed the existence of many species that serve similar ecological roles "ecological redundance" (Walker 1992; Lawton and Brown 1996). "Redundance" is not meant in a pejorative sense, but instead illustrates the importance of similar species being able to compensate functionally (e.g., fixing nitrogen) when another species population has declined (Walker 1995). Ecosystems (and restoration projects) lacking the ecological redundance that characterized the historic condition will be more susceptible to collapse.

ECOTYPE ACCURACY

The biological species concept (Mayr 1942) is inadequate for restoration purposes; rather attention must be given to local genetic variation in organisms known as "ecotypes" (Turesson 1922; Clausen *et al.* 1948). In a discussion of conservation biology, Rojas (1992) writes that, "Considering species as typological entities may … lead workers to disregard geographic variation and to neglect the problem of deciding which level of variability to protect." Rojas concludes that conservation biologists have neglected to understand species concepts relative to their work. We find that applied restorationists also pay too little attention to local, ecotypical variation. However, some writers have addressed the importance of local variation to the success or failure of restoration projects, calling it "the ecotype question" (Cairns 1987).

Scholarly discussion of the ecotype question generally has supported a position of striving for ecotype accuracy. McNeilly (1987) discussed the importance of local ecotypes in heavily degraded areas where plants may have adapted to the extreme toxic conditions of a site, stressing the continuing evolution of plant populations subject to contaminated conditions. Millar and Libby (1989) explored how to maintain a commitment to genetic purity while settling for something less. They note that genetic variation does not necessarily correspond to geographic variation and that one must also consider the microclimatic and edaphic conditions of individuals used for propagules. Proximity does not necessarily denote the appropriate ecotype for a restoration site. Read *et al.* (1996) note that the internal variation of some species (*e.g.*, *E. fasciculatum*) is much greater than others (*e.g.*, *Stipa* spp.) allowing the restorationist to make judgments about the necessity for site fidelity on a case-by-case basis.

Although the consensus seems to be that the restorationist should only collect propagules based on particular knowledge of the plants and locations involved, this precept is motivated by concern that plants themselves will survive and are genetically appropriate. However, *a restoration is not successful if the plants kill the organisms that depend on them.* While a plant of a non-local ecotype may survive when planted as part of a revegetation project, consideration rarely is given to the effects of the plant on other trophic levels. Insects, especially larval forms, give a rough indication of the divergence of different ecotypes.

Consider *Eriogonum fasciculatum*, which is a foodplant for a large number of insects and is widely used in restoration efforts. We have observed that *E. fasciculatum* shows large geographic variation, which often is overlooked in restoration efforts. We know of two restoration sites where a non-local ecotype was established as part of a restoration project (the Defense Fuel Support Point in San Pedro, and upper Newport Bay). At the Defense Fuel Support Point we do not know the source of the non-native ecotype, but it is visibly different from nearby local individuals and is characterized by a depauperate insect fauna, lacking many common species found nearby on the local ecotype. A few examples of the variation within *E. fasciculatum* involve rearing lepidoptera larvae for research purposes. We found a larva of *Hemileuca electra* (a saturniid moth) on *Eriogonum fasciculatum* near Jacumba, CA. It died after being moved to the San Pedro ecotype (Longcore and J. George, unpublished data). Several larvae of *Schinia* sp. collected in Riverside County on *Chaenactis glabriuscula* DC. died at once after consuming the ecotype from the El Segundo sand dunes (Mattoni, unpublished data).[2] To borrow a pun from tropical butterfly ecologist Phil DeVries, using the wrong ecotype "add[s] insult to herbivory" (DeVries and Baker 1989).

Research in the late 1960s and early 1970s by Paul Ehrlich and colleagues (Breedlove and Ehrlich 1968, 1972, Dolinger *et al.* 1973) explains the sensitivity of herbivorous larvae to this intraspecific variation. They found that lupine species (*Lupinus* spp.) subject to herbivory by a lycaenid butterfly (*Glaucopsyche lygdamus*) showed higher levels and compositional variability of alkaloids, compounds that serve as chemical defenses against the larvae. Further, they discovered that variation in alkaloid content and composition between lupine populations of the *same* species was often *higher* than the variation between populations of *different* species. Their work clearly shows the localized nature of the interrelationships between species (in this instance a plant-herbivore complex). For the restorationinst, Ehrlich's work illustrates the enormous importance of ecotype fidelity on the potential ecological function of a restoration site. With the exception of species whose genotypic and phenotypic variation are thoroughly explicated with respect to their associated herbivores, local ecotypes should be used in restoration.

TYPE CONVERSIONS

Finally, we consider habitat type conversions, wherein the restorationist purposefully establishes one habitat type or vegetation association where it was not found historically. Such intentional or inadvertent type conversions constitute a particularly insidious form of historical inaccuracy. Historical accuracy is a difficult goal for restorationists because often little information is available in an accessible format. Jordan and Packard (1987) describe trial-and-error efforts to identify native plant species that would persist under oaks near Chicago. Early efforts had attempted to establish prairie species under the oaks, but further experimentation revealed that another distinct set of plants was adapted to such conditions. After discovering this fact, Packard happened across an 1846 journal called *The Prairie Farmer*, which had identified 108 species characteristic of "barrens," the settler term for natural oak savanna. While Packard was pleased to note that those species corresponded with his list of savanna species, complete historical research could have avoided the frustration of attempting to establish a prairie as the understory of oak savanna in the first place. Because of incomplete historical research, many restorations performed as mitigations may indeed be characterized by a such unintentional type conversions.

Similar examples can be found in southern California in a number of areas. Unfortunately, would-be restorationists obliterate the natural community in their attempts to establish the wrong vegetation type. For example, because of an error misinterpreting the extent of the El Segundo dunes (Arnold 1983:80, 1990:36; see Mattoni 1992:280 for details), some restoration attempts have tried to establish dune scrub vegetation in areas that were historically occupied by the distinct Los Angeles coastal prairie (Mattoni *et al.* 1997). It was only through close observation and historical research completed as part of the El Segundo dunes restoration that the prairie was recognized and described. We hope that the recognition and description of the prairie will inform future restoration efforts on the remaining fragments.

The most well documented instances of type conversions have been done as mitigation under Section 404 permits for the Clean Water Act administered by the U.S. Army Corps of Engineers (Allen & Feddema 1996). In a survey of 75 project sites, Allen and Feddema found that only 67% of the projects had been "successfully completed." Further, they found an overall decrease in wetlands with some types gaining (riparian woodland) while other types declined (freshwater wetland). Distribution of wetland types and overall regional wetland location was changed through the mitigation process. Zedler (1996) also documents and discusses the need for a regional plan to avoid continued replacement of the historic extent of one type of habitat (salt marsh and intertidal flats) with another (deepwater habitat), fueled by mitigation needs.

Conservation and Policy Implications

Our work with the El Segundo blue butterfly created the opportunity to learn what can go wrong in an ecological restoration project. The mistakes identified here occur on a regular basis in projects identified as "restorations." These projects, even when developed under the supervision of the U.S. Fish and Wildlife Service, the California Department of Fish and Game, the California Coastal Commission, or the U.S. Army Corps of Engineers frequently are historically inaccurate and incomplete, and pay little or no attention to ecotype accuracy or type conversions. Examples abound: the plan written for the Deane Dana Nature Center in Friendship Park in Palos Verdes proposes to restore coastal sage scrub with a plant list of about a dozen shrubs (out of approximately 150 plant species that can be identified for the site, many of which are no longer found in adjacent areas and will never recolonize naturally); the Ballona Lagoon "restoration" project commenced by bulldozing all vegetation

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[2] These examples are illustrative only; many other factors may have caused the deaths of the larvae in question, including stress, bacteria, fungi, and viruses. Also, geographic variation between plant individuals may not be genetic, it may result from environmental factors such as differing concentrations of heavy metals in the soil.

(including natives) leaving no chance for ecotype accuracy; the Ballona Wetlands plan developed for the Playa Vista project converts historic salt marsh into a sediment detention basin surrounded by landscaping with native plants bearing little resemblance to the historic community found on the site (in addition to other marine community conversions, historical inaccuracies, and incompleteness).

Such ecologically deficient "restoration" projects could simply be avoided through better communication from the academic community to the resource agencies. Rather than relying entirely on their own overworked staffs, agencies should solicit peer review for restoration plans from qualified experts in the habitats in question who are free from conflicts of interest. Consultants proposing to design and implement restoration projects should be required to pass examinations indicating field identification skills and historical knowledge of the habitats they profess to understand.

One underlying reason for the continued acceptance of deficient restoration planning and implementation is the simple fact that few biologists choose to pursue careers in politics, in which realm many decisions are ultimately made. Rather, the political world tends to select for more people-oriented participants, who, through no fault of their own, lack a robust biological background. When entire elected bodies have not a single biologist in their midsts, they perforce rely on the opinions of others who may or may not have the proper expertise to advise on the issue at hand. Therefore, if ecologists in the academic community would like to see the fruits of their labors translated into more enlightened policy, more outreach to local and regional policymakers will be required.[3] This conference and its predecessor have in some part served that role.

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[3] Perhaps the time has also come for conservation biologists to run for local elected office and to seek positions on planning commissions and similar land-use jurisdictional bodies.

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Taxidea taxus
Author(s): Charles A. Long
Source: *Mammalian Species*, No. 26, Taxidea taxus (Jun. 13, 1973), pp. 1-4
Published by: American Society of Mammalogists
Stable URL: http://www.jstor.org/stable/3504047

MAMMALIAN SPECIES No. 26, pp. 1–4, 4 figs.

Taxidea taxus.

By Charles A. Long

Published 13 June 1973 by The American Society of Mammalogists

Taxidea Waterhouse, 1838

Taxidea Waterhouse, 1838:154. Type species *Ursus labradorius* Gmelin, by original designation.

Taxus Say, 1823:369. Type species *Taxus labradorius*, by monotypy.

CONTEXT AND CONTENT. Order Carnivora, Family Mustelidae, Subfamily Taxidiinae (Long, 1965*b*). The genus includes one Recent species, *Taxidea taxus* (see below), and Pleistocene taxa, possibly species, named *mexicanus* Drescher, 1939, *sulcata* Cope, 1878, *robusta* Hay, 1921, and *papagoensis* Skinner, 1943.

Taxidea taxus (Schreber, 1778)

North American Badger

Ursus taxus Schreber, 1778:520, fig. 142B. Type locality "pays des Esquimaux" from Buffon, 1776:243–244.

Meles Taxus β americanus Boddaert, 1784:80. Type locality North America.

Ursus labradorius Gmelin, 1788:102. A renaming of *Ursus taxus* Schreber.

Meles jeffersonii Harlan, 1825:309. Type locality "open plains of Columbia [River Valley], sometimes those of Missouri [Valley.]"

Taxidea berlandieri Baird, 1858:205. Type locality Llano Estacado, Texas, near boundary of New Mexico.

†*Taxidea marylandica* Gidley and Gaxin, 1933:352. Type locality Cumberland Cave, Allegany County, Maryland. Age Pleistocene.

CONTENT. Long (1972) recognized four Recent and one extinct Pleistocene subspecies as follows:

T. t. taxus (Schreber, 1778:520), see above (*americanus* Boddaert, 1784, *labradorius* Gmelin, 1788, *dacotensis* Schantz, 1946, *iowae* Schantz, 1947, *merriami* Schantz, 1950, and *kansensis* Schantz, 1950, are synonyms).

T. t. jeffersonii (Harlan, 1825:309), see above (*sulcata* Cope, 1878, *neglecta* Mearns, 1891, and *montana* Schantz, 1950, are synonyms, the last according to Long, 1964*b*:371, 1972, and Opinion 897 of the Internat. Comm. Zool. Nomenclature, 1970).

T. t. jacksoni Schantz, 1945:431. Type locality 4 mi. E Milton, Rock Co., Wisconsin.

T. t. berlandieri Baird, 1858:205, see above (*labradoria* Waterhouse, 1838—see Baird, 1858:201, not *Ursus Meles labradorius* Gmelin, 1788, *californica* Gray, 1865, *infusca* Thomas, 1898, *phippsi* Figgins, 1918, *robusta* Hay, 1921, *sonoriensis* Goldman, 1939, *papagoensis* Skinner, 1943, *apache* Schantz, 1948, *littoralis* Schantz, 1949, *hallorani* Schantz, 1949, and *nevadensis* Schantz, 1949, the last renamed *halli* Schantz, 1951, are synonyms).

T. t. marylandica Gidley and Gazin, 1933 (see Long, 1964*a*). Type locality Cumberland Cave, Maryland, Pleistocene. Regarded as a distinct species by the authors, and as inseparable from *T. t. taxus* by Hall (1944).

FIGURE 1. North American badger from Ibapah, Utah. In the southernmost subspecies, unlike the specimen shown, the dorsal whitish stripe extends to the base of the tail. Note the "badges" on the face, and the fossorial foreclaws. Photo by R. Porter.

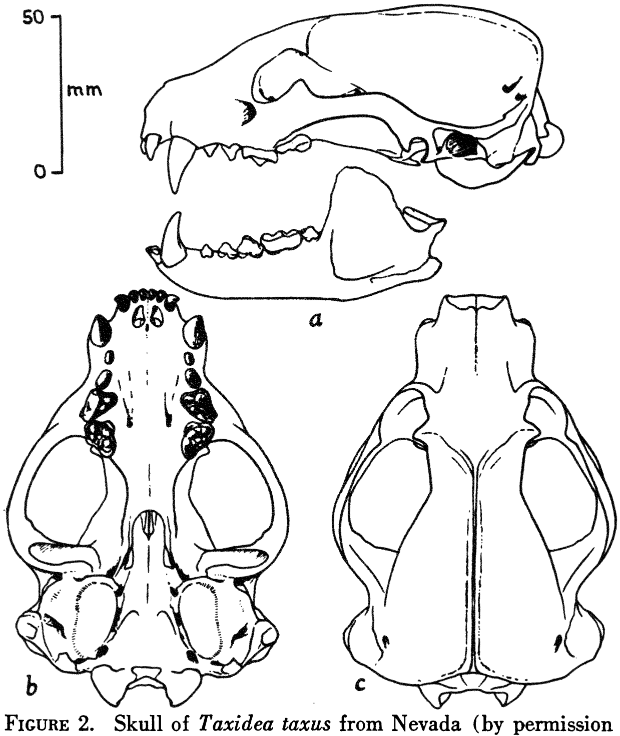

FIGURE 2. Skull of *Taxidea taxus* from Nevada (by permission of Professor E. Raymond Hall, from Hall, 1946:215). Lateral view of skull and lower jaw (a), ventral view (b), and dorsal view (c).

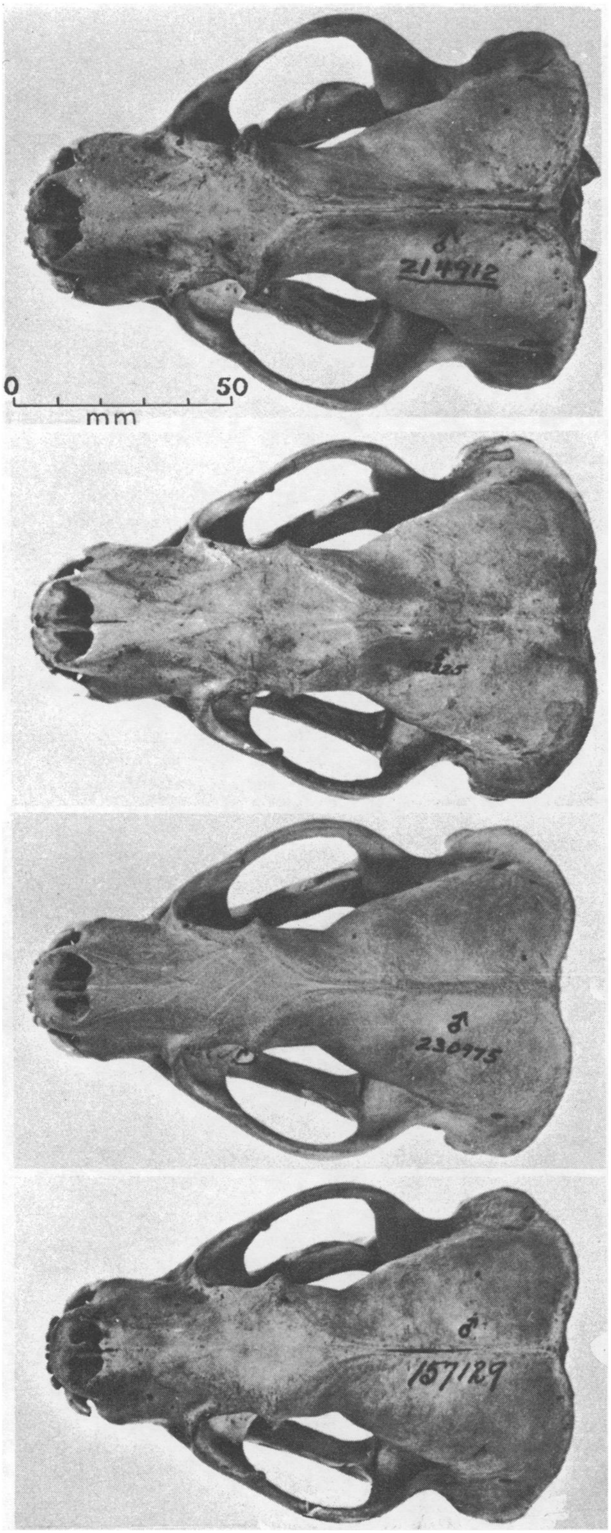

FIGURE 3. Skulls of the four Recent subspecies of *Taxidea taxus*. From top to bottom these are: *T. t. jeffersonii*, male from Dillon, Montana; *T. t. taxus*, male from Carmen, Manitoba; *T. t. jacksoni*, male from Mamie Lake, Wisconsin; *T. t. berlandieri*, male from San Luis Mountains, Chihuahua. All skulls in U. S. National Museum.

DIAGNOSIS. The following diagnosis refers to both genus and species. Upper molar subtriangular, nearly right-angled with hypotenuse posterolateral; carnassial premolar also subtriangular with longest side posteromedial; skull wedge-shaped, broad posteriorly; auditory and mastoid bullae large; skull varying from 113 to 141 mm in length; frontals in juveniles escutcheon-shaped, fused in adults; body depressed and stout, legs short; feet subdigitigrade, with long curved foreclaws and shovel-like hind claws; toes of forefeet partially webbed; nictitating membrane can cover eye; pelage shaggy, grayish or brownish with white medial stripe on head, extending to base of tail in *berlandieri*; feet black or brown; "badges" of black on face surrounded by white; eight mammae; penis large, bearing scalloped projection distally; baculum hooked and twisted; adult dentition i 3/3, c 1/1, p 3/3, m 1/2, total 34; deciduous dentition di 1 or 2/0, dc 1/1, dp 3/3, total 18 or 20. Weights in large northern badgers up to 26½ pounds (12 kg) in males, which are larger than females. After Coues (1877) and Long (1965*b*, 1969, and 1972). See figure 1 for external view of *Taxidea taxus* and figure 2 for cranial details; dorsal views of the skulls of four Recent subspecies are shown in figure 3.

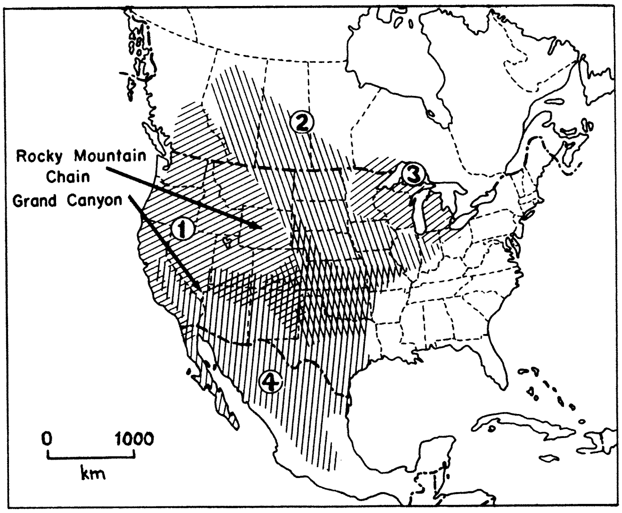

FIGURE 4. The distribution of *Taxidea taxus* in North America. Subspecies are: 1, *T. t. jeffersonii*; 2, *T. t. taxus*; 3, *T. t. jacksoni*; 4, *T. t. berlandieri*. Cross hatching shows areas of intergradation. The Rocky Mountains and the Grand Canyon seem important in the differentiation of the western subspecies.

GENERAL CHARACTERS. Total length is about 600 to 730, length of tail vertebrae is 105 to 135, and length of hind foot ranges from 95 to 128. Other descriptions may be found in Audubon and Bachman, 1847; Baird, 1858; Coues, 1877; Mearns, 1891, Pocock, 1920, 1925; and Seton, 1929, which include photographs, measurements, and drawings. Long and Long (1965) described dental variations; and Long (1965*b*) the juvenile skull and the relationship with *Meles*.

DISTRIBUTION. The geographic range of the four Recent subspecies listed above is mapped in figure 4. Fossil occurrences in Alaska (Péwé, 1957), Maryland and New York (Gidley and Gazin, 1933), and Kentucky (Guilday, 1968), reveal profound distributional shifts in the Pleistocene. The altitudinal range is below sea level (Death Valley) to about 3660 m (12,000 feet). Ordinarily found in the treeless habitats of Transition and Upper Sonoran life-zones, the badger is known from Arctic-alpine down to the lower Austral Life-zone. Presently the badger is expanding its range eastward (Lyon, 1932; Snyder, 1935; Leedy, 1947; and Nugent and Choate, 1970).

FOSSIL RECORD. *Taxidea* has been reported from the late Pliocene (Bjork, 1970; Hibbard, 1941; Drescher, 1939); most workers regard assignment of these remains to *T. taxus* as questionable, and others regard some of the deposits as possibly Pleistocene. Some Pleistocene records have been mentioned above and by Long (1972). *Pliotaxidea* Butterworth is probably close to the ancestral line of Recent badgers (Hall, 1944).

FORM. Hall (1927) described the musculature in *Taxidea*. Long and Frank (1968) discussed the form and variation of the baculum, and Long (1969) discussed the gross anatomy of the penis. Pocock (1920, 1925) and Long (1965*b*) described cranial form in *Taxidea taxus*, and Long (1965*a*) discussed jaw articulation and tooth wear. Wright (1966, 1969) described the form and tissues of the internal reproductive organs and accessory glands.

FUNCTION. Hardly anything is known about the physiology of *Taxidea*. At high elevations and latitudes badgers are torpid in winter, but probably are not true hibernators (Audubon and Bachman, 1847:366; Hamilton, 1939:134). They emerge on days of thaw (Seton, 1929; B. Bailey, 1929).

ONTOGENY AND REPRODUCTION. After mating in summer and early autumn (Davis and Robertson, 1944:264, Wright, 1966, 1969) impregnation occurs in females older than 1 year, and occasionally in juvenile (4 to 5 months) females (see also Hall, 1946:222). Usually three follicles ovulate (Wright, 1966). Implantation is delayed, development arrested in the blastula stage until between December and February (Hamlett, 1932:285–6) in Kansas, and until February in western Montana and South Dakota. Spermatogenesis lasts from May through August, and yearling males do not breed. Young are born in March and early April, furred and blind. Lactation occurs through June, and there is no post-partum estrus or further ovulation. Schwartz and Schwartz (1959:294) listed a maximum of seven embryos, but this record needs verification. Wright (1969) discussed the use of bacular length and annuli of lower canines and jaw in determining age. The badger lives in captivity to about 11 years, one living 13 years, 10 months, and 14 days (Flower, 1931:177). Jackson (1961:367) mentioned a life span of 15 years and 5 months. The changes with age in the skull are profound (Shufeldt, 1922). Self-sharpening and bracing of worn canines were discussed in relation to the hinge-locking mechanism of the jaw articulation by Long (1965*a*). Long (unpublished) has in manuscript remarks on the ontogeny of the skull, molting, and growth.

ECOLOGY. Badger parasites include a variety of nematodes (Ortlett, 1922:1107; Herman and Goss, 1940; Kalkan and Hansen, 1966; Keppner, 1969*a*; Tiner, 1953; Leiby *et al.*, 1971; Worley, 1961), tapeworms (Rausch, 1947; Keppner, 1967, 1969*b*; Leiby *et al.*, 1971), flukes (Swanson and Erickson, 1946; Leiby *et al.*, 1971), mallophaga (Emerson, 1964:163), fleas (Fox, 1940:45; Ellis, 1955; and Hubbard, 1947:502) and ticks (Hubbard, 1947; Ellis, 1955; Gregson, 1956). Jackson stated that badgers are susceptible to rabies and tularemia. Some predation occurs on badgers by coyotes (Seton, 1929) and golden eagles (G. B. Grinnell, 1929). Today a great deal of mortality is caused by automobiles, guns, poisons, and traps. Density, vaguely estimated, has been reported as one badger per 2.6 square kilometers (square mile) and 10 dens per square mile (Seton, 1929). V. Bailey (1905) mentioned a badger spending a summer in a 20-acre (0.8 km^2) field. Radio tracking has been attempted but few results are available. Sargeant and Warner (1972) reported data from radio-locations of a single female badger from summer into winter. "Overall home range" was determined as 850 hectares, and home range varied from 725 hectares in summer, to 53 in autumn, and to only 2 in winter. Usually the female dug a new den each day in summer, but reused dens considerably in autumn, and thereafter maintained a single den at least until 9 January. Burrows are used for dens, escape, and predation. Snead and Hendrickson (1942:389) described badger burrows. Foods are varied and include many small vertebrates, especially rodents (Errington, 1937; Snead and Hendrickson, 1942; Hamilton, 1939). Even fish, snakes, insects, honey combs, bees, and larvae, and bank swallow broods are eaten (Drake and Presnall, 1950; Jackson, 1961:368; Grinnell *et al.*, 1937; Potter, 1924).

BEHAVIOR. The badger is reportedly active both day and night, and is exceedingly fossorial (Audubon and Bachman, 1847:365; Seton, 1929; Perry, 1939). It presents a ferocious appearance to enemies, emitting aggressive sounds described by Seton. Other "purring" sounds were described by Perry. The anal glands may be used in defense (Grinnell, *et al.*, 1937). Males are solitary, except in the mating season, and females are usually so except when mating or rearing young. Davis (1946:175) suggested that the badger is not monogamous. Badgers may team with coyotes to catch rodents (Seton, 1929; Cahalane, 1950). The badger is a good swimmer (Seton, 1929; Wood, 1921). Reportedly the badger buries its dung (Walker *et al.*, 1964), although scats are often figured, presumably not buried. Play of the young and of captive badgers has been described by Seton, 1929; Audubon and Bachman, 1847:364; Perry, 1939; and Fry, 1928. Predation by one badger on ground squirrels was accomplished by lurking within a burrow (Balph, 1961).

REMARKS. Nothing is known about genetics of *Taxidea*. *Meles alba* Brisson (1762), type locality "Eboraco novo," known as "le Blaireau Blanc" was an albino raccoon according to Desmarest as reported by Richardson (1829:38). "Badgering" and "badger-baiting" with dogs was done chiefly with the old world badger *Meles*, but also with *Taxidea* according to Coues, 1877:283. The badger is exceptionally valuable to man as a predator on injurious rodents.

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From: Wilson Bull., 101(4), 1989, pp. 606-620

BIRD-WINDOW COLLISIONS

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ABSTRACT. — Collisions of birds with windows were studied by reviewing the literature, collecting data from museums and individuals, monitoring man-made structures, and conducting field experiments. Approximately 25% (225/917) of the avian species in the United States and Canada have been documented striking windows. Sex, age, or residency status have little influence on vulnerability to collision. There is no season, time of day, and almost no weather condition during which birds elude the window hazard. Collisions occur at windows of various sizes, heights, and orientations in urban, suburban, and rural environments. Analyses of experimental results and observations under a multitude of conditions suggest that birds hit windows because they fail to recognize clear or reflective glass panes as barriers. Avian, manmade structural, or environmental features that increase the density of birds near windows can account for strike rates at specific locations. A combination of interacting factors must be considered to explain strike frequency at any particular impact site. *Received 28 Oct. 1988, accepted 17 April 1989.*

The earliest account of a bird hitting a window in North America is by Nuttall (1832:88). He described a Sharp-shinned Hawk (*Accipiter striatus*) which, in the pursuit of prey, flew through two panes of greenhouse glass only to be stopped by a third. Townsend (1931) described a series of five fatalities of the Yellow-billed Cuckoo (*Coccyzus americanus*). His paper was the first to suggest that avian vulnerability to windows may be more marked in some species than in others and that specific windows claim a succession of victims. He termed the victims "tragedies" and apparently regarded them as rare, self-destroying incompetents. Picture windows were relatively uncommon through the end of World War II, and there was little reason for concern about their threat to birds. In the postwar period, a building boom stimulated the rapid expansion of the sheet glass industry, and large glass windows were incorporated into the designs of new and remodeled structures. Today, it is not uncommon to find modern buildings that are entirely surfaced with glass.

I found 88 papers reporting bird-window collisions, primarily after the mid-1940s (Klein 1979). They document strikes in North America, South America, West Indies, Europe, and Africa, and, with few exceptions are cited in annotated bibliographies on man-caused mortality to birds (Weir 1976, Avery et al. 1980). However, most textbooks and encyclopedia treatments of ornithology present little, if any, description of the fatal hazards that windows pose to birds. The sheet glass industry and its commercial allies appear to be unaware of the problem. On the other hand, I found avian fatalities resulting from window strikes to be common knowledge among the general public.

Birds have been reported to strike two general types of windows as classified according to their visual effects on the human eye. These are transparent windows which appear invisible and reflective windows which mirror the facing outside habitat. Two general types of collisions have been described (Wallace and Mahan 1975:456) and both reveal the ability of glass to misinform and misguide at least some birds. One primarily involves birds such as Northern Cardinal (*Cardinalis cardinalis*) that commonly flutter against picture windows and harmlessly peck the glass during the spring and summer. These birds seldom, if ever, stun or injure themselves or shatter the glass and usually are males defending their territories against their reflected images. In the second type, birds fly into transparent or reflective windows as if unaware of their presence. These collisions often have fatal consequences, and are the subject of this paper.

In this paper my objectives are: (1) to propose an explanation for why birds collide with windows, (2) to describe and analyze species, environmental and manmade structural characteristics associated with bird-window collisions in the United States and Canada, and (3) to suggest how these select characteristics account for the differential frequency with which birds strike windows in various man-made structures.

METHODS

I collected data for this study from 1974 to 1986 from personal observations, records of cooperating individuals, and a series of field experiments. A form letter was sent to 466 curators of museums and I I individuals in the United States and Canada. They were asked to identify birds salvaged as window-kills or noted as surviving window strikes in 1975 and 1976; a few respondents included additional data from 1963 to 1977. Of those surveyed. 208 responded: 125 listed species known or reported to have collided with windows and 13 estimated the number of collision casualties brought to them each year, although they did not indicate the species. I obtained data from: (1) salvaged window-kills that were placed in the Dept. of Zoology Bird Collection at Southern Illinois University at Carbondale (SIUC) between 1971 and 1974 (currently in the Dept. of Biology bird collection at Muhlenberg College, Allentown, Pennsylvania), (2) Jack and Muriel Hayward's house in the Union Hill community located 5.7 km southwest of Carbondale, Jackson County, Illinois, and (3) several private homes and university and commercial buildings within a 52,300-h area in and around Carbondale, Illinois. The Hayward house was the only building at which bird strikes were recorded systematically in southern Illinois. The home was checked by the occupants, often several times a day, from September 1974 through December 1976. The house stands on a slope and is surrounded by shrubs, mixed conifer and deciduous trees, fields and lawn. It has 52 windows ranging in size from 0.6 m wide by 0.9–2.2 m high with a total outer glass surface area of 114.3 m^2. Each window was individually numbered to accurately register the location of bird strikes. As with the Hayward home, detailed data were obtained from the residence of Polly Rothstein in southeastern New York, 1.6 km southeast of Purchase, Westchester County. Except for short periods, a few hours to 1-2 days, she collected data from August 1975 through December 1976. The Rothstein house is located in a suburban setting on level ground and is surrounded by trees, shrubs, and lawn. Bird collisions were documented whenever a strike was heard or seen, or a specimen was found beneath a window. Although most reports lacked some information, the data recorded were species, temporal, and habitat variables. Specimens salvaged at the Rothstein house were given to the Bruce Museum, Greenwich, Connecticut.

Four field experiments were conducted to determine if birds can recognize transparent obstructions or reflections. All experiments were conducted on the farm of W. G. George in the Shawnee Hills, 1.7 km north of Cobden, Union County, Illinois. Typical of small farms in this area, the land has patches of woods and fields, a small apple orchard, a sizeable lawn around the farmhouse, a corn field, and two water impoundments. Two preliminary experiments, conducted over 8- and 13-day periods (8-15 November and 19 November-1 December 1976), were designed to determine if birds would strike clear and reflective glass not associated with man-made structures. A strike was registered when a specimen was found beneath a window or a feather, body smudge or blood smear was found on the glass. In the first experiment, six clear storm windows, 0.4 m wide by 1.2 m high, having a combined surface area of 2.9 m^2 were placed on the ground adjacent to one another (separated by 0–15.2 cm) and on the periphery of a woody thicket facing an old field habitat. When viewed from the field or the thicket, habitat was visible behind each pane. In the second experiment, a mirror, 0.6 m x 1.7 m high, simulated a reflective glass pane. It was placed in the same locality as the clear panes and appeared to reflect perfectly the field habitat and sky. During both experiments the glass was checked daily. The third experiment, conducted over a 20-day period (19 March-7 April 1977), was designed to determine if birds would strike clear picture windows simulating those in new houses and erected in a habitat where no other man-made structure previously existed. Five identical wood-framed windows, 1.4 m x 1.2 m high, with their bases 1.2 m above ground, having a combined surface area of 8.5 m^2 were constructed on the edge of a wooded area and corn field (Fig. 1). Windows were placed along a tree line running east to west and facing north-south. Distance between windows from cast to west (right to left in Fig. 1) were 12.9 m, 16.5 m, 15.7 m, and 23.8 m. Depending on the light conditions and angle of view, habitat was seen behind or reflected from the glass, or a combination of these effects was visible. Trays were placed under each window to catch collision casualties. Each window was checked daily.

Fig. 1. Field experiment study site in Cobden, Union County, Illinois.

The fourth experiment, conducted over a 1-year period (21 February 1977-21 February 1978), was designed to determine if birds would strike clear and reflective windows that were placed in an existing structure (a century-old barn) that previously had no windows. Two clear and two gray-tinted panes, 1.4 m wide by 1.2 m high, having a combined surface area of 6.8 m^2, were installed with their bases 3.8 m above the ground on the north and east sides of the barn. From outside, wooded habitat was visible on the other side of the barn when looking through both clear panes. When viewed from an angle that did not permit a view through both panes, the clear windows reflected the facing wooded habitat. The tinted panes were adjacent to the clear panes, and they appeared to reflect perfectly the facing wooded habitat. Trays were placed under each window to catch collision casualties. Each window was checked daily.

Data were compared and analyzed with binomial and Chi-square tests (Siegel 1956). In some analyses, the data were subdivided to determine if they showed chronological trends.

RESULTS

Species. — My survey revealed 225 species belonging to 42 families are known to have struck windows. This number represents 25% of the 917 species that occur in the two countries (A.O.U. 1983). Table 1 lists the 20 most frequently reported species in the survey. In general, the diversity of collision victims include species that occupy every major habitat type. Absent from the fist are birds that rarely occur in habitats containing man-made structures. They include most waterbirds, soaring hawks, and terrestrial species occupying unpopulated or sparsely populated desert, grassland, and forest. Species accounting for most strikes at single residences were similar to those in the survey. Exceptions were relatively large numbers of Yellow-billed Cuckoo collisions at the Hayward house and Blue Jay (*Cvanocilta cristata*) and House Sparrow (*Passer domesticus*) strikes at the Rothstein house.

TABLE 1

SPECIES[a] MOST FREQUENTLY REPORTED STRIKING WINDOWS IN UNITED STATES AND CANADA

- American Robin (*Turdus migratorius*)
- Dark-eyed Junco (*Junco hyemalis*)
- Cedar Waxwing (*Bombycilla cedrorum*)
- Ovenbird (*Seiurus aurocapillus*)
- Swainson's Thrush (*Catharus ustulalus*)
- Northern Flicker (*Colaptes auratus*)
- Hermit Thrush (*Catharus guttatus*)
- Yellow-rumped Warbler (*Dendroica coronata*)
- Northern Cardinal (*Cardinalis cardinalis*)
- Evening Grosbeak (*Coccothraustes vespertinus*)
- White-throated Sparrow (*Zonotrichia albicollis*)
- Ruby-throated Hummingbird (*Archilochus colubris*)
- Tennessee Warbler (*Vermivora peregrina*)
- Yellow-bellied Sapsucker (*Sphvrapicus varius*)
- Purple Finch (*Carpodacus purpureus*)
- Common Yellowthroat (*Geothlvpis trichas*)
- Rose-breasted Grosbeak (*Pheucticus ludovicianus*)
- Gray Catbird (*Dumatella carolinensis*)
- Wood Thrush (*Hvlocichla mustalina*)
- Indigo Bunting (*Passerina cyanea*)

[a] Species reported most often in a survey of 125 museum curators and individuals: most frequent is listed first.

Age and sex. — Window casualties were analyzed for age and sex differences by comparing pooled species data for all of southern Illinois, at a single residence (Hayward house), and for select species with sample sizes of ten or more (Table 2). Passerine ratios of immature (hatching-year, HY) to adult (after-hatching-year, AHY) birds were expected to be 3:1 if the samples were representative of populations immediately after the breeding season (Lack 1954, Peterson 1963). Except for the Purple Finch (*Carpodacus purpureus*), there were no significant differences from the expected ratio (Binomial test, $P > 0.05$). Counts for the Purple Finch differed significantly from the 3:1 ratio (Binomial test, $P < 0.03$), but adults and immatures were killed with equal frequency; adults of this species may be more vulnerable than immatures or they may have occurred in proportionately greater numbers at this particular site. These data suggest that adults and immatures are at least equally vulnerable to windows. Male and female strike rates did not differ significantly from the expected 50:50 ratio for pooled or individual species data (Binomial test, $P > 0.24$).

TABLE 2
AGE[a] AND SEX[b] OF WINDOW CASUALTIES

	Age			Sex		
Pooled[c]/individual[d]	N	AHY	HY	N	M	F
Southern Illinois	72	17	55	191	91	100
Hayward House	22	8	14	56	25	31
American Robin				10	7	3
Northern Cardinal				is	7	11
Dark-eyed Junco	11	4	7	12	5	7
Purple Finch	18	9	9	18	6	12

[a] Age was determined by skull pneumatization and limited to AHY (after hatching year) and HY (hatching year) passerines killed in fall (September to December).

[b] M = male; F = female.

[c] Southern Illinois data obtained from casualties at several buildings around Carbondale, Jackson County; Hayward house data obtained from single residence.

[d] Species with sample sizes of 10 or more.

Seasons.— Strike data from several buildings in southern Illinois and at single residences of the Hayward and Rothstein houses were analyzed by season (Fig. 2). The frequency of strikes per month were not uniformly distributed for southern Illinois in 1975 ($x^2 = 27.6$, $P < 0.01$) or 1976 ($x^2 = 50.0$, $P < 0.001$), for the Hayward house in 1975 ($x^2 = 35.5$, $P < 0.001$), or the Rothstein house in 1976 ($x^2 = 32.9$, P < 0. 00 1). Seedeaters; attracted to feeders near windows accounted for high numbers of strikes in winter (December-February). Migrants, especially nocturnal migrants, active around dwellings during the day, accounted for high strike rates in spring (March-May) and fall (September-November). Breeding birds, especially the Yellow-billed Cuckoo, accounted for summer (June-August) strikes. These data suggest that birds strike windows in every season of the year, that collision rates may vary greatly from month to month, and except for a reduction during summer breeding, no marked seasonal differences are evident.

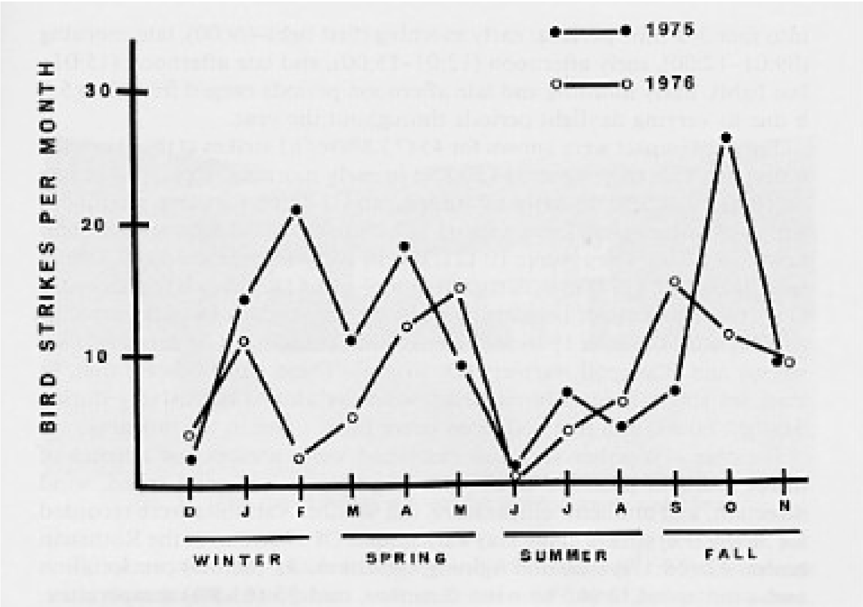

Fig. 2. Seasonal distribution of frequency of bird strikes at windows in southern Illinois.

Times of day. — To compare diurnal collision rates, a day was divided into four 3-h time periods: early morning (first light-09:00), late morning (09:01-12:00), early afternoon (12:01-15:00), and late afternoon (15:01-last light). Early morning and late afternoon periods ranged from 2 to 5.5 h due to varying daylight periods throughout the year.

Times of impact were known for 45 (73.8%) of 61 strikes at the Hayward house in 1975; they were: 31 (50.8%) in early morning, 8 (13.1%) in late morning, 5 (8.2%) in early afternoon, and 1 (1.6%) in late afternoon. Times of impact were known for 41 (87.2%) of 47 strikes at the Rothstein house in 1976. They were: 10 (21.3%) in early morning, 19 (40.4%) in late morning, 8 (17.0%) in early afternoon, and 4 (8.5%) in late afternoon. Only two accounts of impacts at night were recorded. Both occurred at the Hayward house in 1976 and were by Black-throated Green (*Dendroica virens*) and Blackpoll warblers (*D. striata*). These data indicate that, at least for single homes, birds strike windows almost exclusively during daylight hours, and that collisions occur more often in the morning.

Weather. — Weather variables examined were: presence or absence of direct sunlight, presence or absence of precipitation, wind speed, wind direction, and ambient temperature. All weather variables were recorded for 36 (59.0%) strikes at the Hayward house. Of 47 strikes at the Rothstein house, 32 (68.1 %) included lighting condition, 31 (66.0%) precipitation and wind speed, 2 (4.3%) wind direction, and 30 (63.8%) temperature. The percentages used in the weather analysis refer to these documented records.

Strike rates were substantial at both houses during both sunny and overcast conditions; under sunny conditions, 24 (66.7% and 75.0%) collisions were recorded at both the Hayward and Rothstein houses. All but one strike, during rain at the Rothstein home, occurred in the absence of precipitation. In southern Illinois, three additional strikes were documented in rain. During a severe snowstorm approximately 50 non-fatal bird strikes were recorded when a flock of Dark-eyed Juncos (*Junco hyemalis*) flew into a window of a rural home in Makanda, Illinois, in 1976. Birds struck windows under varying wind speeds, but collisions were recorded most often during calm conditions; 33 (91.7%) and 23 (74.2%) collisions occurred in winds of 0-11.3 kph (0-7 mph) at the Hayward and Rothstein houses, respectively. At the Hayward house five or more strikes occurred at windows facing all major compass directions. Similarly, for both houses, collisions occurred in temperatures ranging from -9.4-31.1C (15.1-88.0F). Comparison of the frequency of strikes in four equal categories of the temperature range for each house revealed that three (10.0%) or more occurred in each category. The overall weather data indicate that, with the exception of certain severe conditions affecting visibility, strike rates are higher during favorable weather.

FIG. 3. Clear glass windows of a corridor showing see-through effect.

Windows and man-made structures. — Bird strikes occurred at windows with clear transparent panes and at those with tinted reflective panes. When clear windows are installed one behind the other, such as in corridors, stairways, or rooms, they create an illusion of an unobstructed passageway (Fig. 3). Tinted windows create an illusion of unobstructed habitat which is mirrored on the glass surface. Clear panes mimic tinted mirror-like panes when little or no light is visible behind them (Fig. 4). Except for a seemingly related incident of frightened individuals hitting the side of a home, I found or collected no records of strikes at opaque, translucent, or stained glass windows which present other visual effects. At one site, over a 5-year period (1975-79), one account documented a strike at a reflective glass door but none at the adjacent stained glass windows of a church in Madison, Illinois (V. Lecko pers. comm.).

Strikes occurred at windows of various sizes, in structures of many different sizes and shapes ranging from those installed in stationary motor vehicle doors and telephone booths, to large plate glass walls around multistory buildings. Collisions were documented at windows of buildings located in urban, suburban, and rural environments. These data qualitatively indicate that collisions are likely at any outside clear or tinted window installed in any structure located in any type of habitat.

Quantitatively, 1975 data from the Hayward house were used to analyze strikes at windows of different sizes, heights from the ground, and orientation. Window size was known for 53 (86.9%) and window height for 49 (80.3%) strikes (Table 3). These data indicate that collisions occur at windows of different sizes and heights from the ground. Collisions may be more frequent at large windows (>2 m^2 [21.6 ft^2]) placed at ground level and above 3 m (10 ft). Window orientation was known for 49 (80.3%) strikes, Strikes per square meter of glass for each facing direction were: 0.5 northeast, 0.1 southeast, 0.9 south, 0.4 southeast, and 0.7 west and northwest. During fall and spring, windows that cut across and faced migratory flightpath directions, north and south respectively, were suspected of posing a greater hazard to migrants than windows facing east or west. To test this hypothesis, only migrants in southern Illinois were considered and consisted of 14 fall and three spring migrants at the Hayward house in 1975 and 1976. As might be expected for fall migrants, eight (57.1%) struck windows oriented northwest, but five (35.7%) hit southwest, and one (7.1%) struck a west facing window (Binomial test, $P = 0.79$). Only one (33.3%) spring migrant hit a window oriented southwest while two (66.7%) others struck windows facing northwest. Comparison of strikes per square meter of glass showed no marked tendency for south or north bound migrants hitting north or south facing windows, respectively. These data indicate that windows facing general migratory directions of north and south are no more hazardous than windows oriented in other directions.

Experiments. — Two experiments tested the hazards of clear and reflective glass not associated with man-made structures. Over an 8-day period, four birds died after colliding with clear windows; they were: two Northern Cardinals, a Red-bellied Woodpecker (*Melanerpes carolinus*), and a White-throated Sparrow (*Zonotrichia albicollis*). Over a 13-day period, two birds died after hitting a mirror simulating a reflective pane, a White-throated

Sparrow and a Dark-eyed Junco. Strikes at the mirror were probably minimal due to ice covering the surface during early morning hours throughout the experiment. These results indicate that windows need not be associated with man-made structures to kill birds.

FIG. 4. Clear glass of Hayward house showing reflective effect.

The third experiment, monitoring five clear picture windows simulating those in new houses, resulted in 13 strikes over a 20-day period. Eight (65%) were fatal, the birds killed were: Northern Cardinals, two; Dark-eyed Juncos, four; Fox Sparrow (*Passerella iliaca*); and Swamp Sparrow (*Melospiza georgiana*). These data further suggest that birds may fail to detect transparent windows in man-made structures.

In the fourth experiment, seven strikes were recorded over a I-year period at clear and reflective windows installed in a century-old barn. Bay-breasted Warbler (*Dendroica castanea*) and three unidentified birds hit clear windows; American Robin, Dark-eyed Junco and one unidentified bird hit reflective windows. These results further document that glass panes become hazardous for birds once installed in man-made structures, regardless of how long the structure may have been a part of the surrounding environment.

TABLE 3
BIRD COLLISIONS[a] AT WINDOWS OF DIFFERENT HEIGHTS[b] AND SIZES

Height (m)	Size								
	Small (<1 m^2)			Medium (1-2 m^2)			Large (>2 m^2)		
	N	Arca(m^2)	N/m^2	N	Area(m^2)	N/m^2	N	Area (m^2)	N/m^2
0.0-0.3	0	0.0	0.00	0	0.0	0.00	22	43.4	0.51
0.3-3.0	2	6.3	0.32	0	8.5	0.00	2	11.7	0.17
>3.0	0	6.9	0.00	0	8.7	0.00	23	29.0	0.79

[a] Data from a single residence, the Hayward house, Carbondale, Jackson County, Illinois

[b] Height is distance from ground to base of pane.

DISCUSSION

Why birds strike windows. —The literature contains several hypotheses attempting to explain how windows may be rendered functionally invisible to birds. If we exclude the harmless collisions resulting from territorial residents fighting their mirror images, all other hypotheses can be grouped into two causal categories. One group consists of defective, impaired, or deceived hypotheses. Several authors have speculated that birds hit windows because of: (1) defective eyes (Willet 1945), (2) impaired vision due to smoke (Langridge 1960), blinding glare (Sinner unpubl. data), mist (Konig 1963), alcohol (Rogers 1978), or diverted attention (Dunbar 1949, Giller 1960, Bent 1968:231, Raible 1968, Valum 1968). None of these explanations are supported by my results. Field experiments revealed that birds collide with: (1) clear and reflective windows not installed in manmade structures, (2) clear windows installed in structures simulating those in new houses and placed in habitats where no other human dwellings previously existed, and (3) clear and reflective windows installed in an existing structure which had been a part of the habitat for more than a century. Individual accounts further document that birds strike windows of various sizes, heights from the ground, and orientation in man-made structures of various shapes and sizes that are set in urban, suburban, and rural environments. These data suggest that windows are not recognized as obstacles by birds, whether installed in man-made structures or placed in their accustomed haunts.

The second group of hypotheses emphasize perception. A number of authors have speculated that inexperienced birds strike windows (Bauer 1960, Giller 1960, Morzer-Bruijns and Stwerka 1961, Löhrl 1962, Raible 1968, Valum 1968, Schmitz 1969, Harpum 1983). There is no evidence indicating that physical deficiencies of the young or learning in adult or immature solely determines the ability of birds to detect glass barriers. Immatures and adults were found to be equally vulnerable, and the diversity of window-kills suggest no species is immune from the hazards of glass. Although indirect. available evidence supports the interpretation that the avian visual system is incapable of perceiving clear and reflective glass (Gibson and Walk 1960, Walk and Gibson 1961, Emlen 1963, Tallarico and Farrell 1964).

My observational data indicate that there is no exclusive avian vulnerability to windows based on age or sex, season, time of day, weather, window type or setting. Experiments further document that birds do not discriminate between unobstructed habitat and habitat seen behind clear glass or mirrored in reflective panes. Overall, these findings indicate that birds are likely to strike windows wherever they mutually occur. In general, glass is an invisible and potentially lethal hazard for all birds, but especially for those in flight. Other animals (insects, fish, mammals) are known to frequently strike stationary windows or other glass barriers, but the momentum at which they impact usually does not cause serious injury. In contrast, even the smallest flying bird can generate fatal momentum.

Factors influencing collision frequency. — Since glass is invisible to birds, various bird, window, and environmental characteristics may explain the frequency with which certain species become casualties at particular localities. Strike rates at specific sites are unique and require attention to a combination of contributing factors. However, some factors can substantially influence the species and frequency of collisions. Considering the importance of single factors is a means of dealing with a complex problem, and knowing the importance of a factor can help assess and suggest measures to reduce or eliminate strikes at a particular site.

Bird-related factors include density and behavior. Although other factors were examined in their analysis, Graber and Graber (unpubl. data) found that the total number of birds in the area was correlated with the number of collisions at their rural Pope County home in southern Illinois ($r = 0.83$, $N = 10$, $P < 0.005$). Flight habits of birds accustomed to manmade structures may provide some protection by reducing the force with which the strike occurs. House Sparrow, European Starling (*Sturnus vulgaris*), and Rock Dove (*Columba livia*) seem to avoid windows by hovering in front of or slowly flying to nearby perches. However accustomed these species are to human dwellings, they are killed frequently at some sites. R. F. Johnston (pers. comm.) reports Rock Dove flying against small, cave-like windows at the Museum of Natural History, Univ. of Kansas. Hummingbirds learned to avoid the glass sides of cages (Bent 1940:386), and individuals accustomed to living near buildings may benefit from non-fatal collisions by learning to avoid the space that windows occupy. If this type of learning occurs in the wild, it may serve to protect at least some individuals, but it is likely to be of limited consequence for most species. Some birds are reported to be at high risk due to their habit of flying, through restricted passageways in heavy cover (Ross 1946, Snyder 1946); they are killed while attempting to reach lighted areas behind or reflected in glass and often consist of Accipiter hawks, grouse, thrushes, and waxwings. Others habitually fly through open doors and windows, thus increasing their vulnerability (Löhrl 1962). Many accounts document distracted individuals as frequent victims: individuals chasing one another (Dunbar 1949), individuals escaping danger (Valum 1968, Schmitz 1969), predators pursuing prey (Klem 1981), and individuals under the influence of alcohol (Rogers 1978), or spatially disoriented due to a combination of adverse weather and artificial lighting (Herbert 1970).

Window-related factors influencing strike rate include type, size, placement of glass, and the presence of bird attractants. I found birds more vulnerable to clear or reflective large (>2 M^2) windows at ground level and at heights above 3 m. With respect to location, birds hit windows wherever they occur, but strike rates were highest in suburban and rural environments, which, in most cases, typically contain the largest densities.

Similarly, bird attractants were found to influence the frequency of strikes by increasing bird density near windows. Attractants are feeders, fruiting trees and shrubs, water supplies in the form of bird baths and impoundments, nesting or perching sites in vegetation, and areas that offer protection from adverse weather conditions. The frequency with which finches, blackbirds, chickadees, titmice, nuthatches, woodpeckers, and hummingbirds were reported as victims is probably best explained by their regular and abundant occurrence at feeders.

Environmental factors influencing strike rate include season, time of day, and weather. The frequency of strikes in different seasons is probably best explained by the seasonal abundance of birds in human-modified environments. I found seasonal strike rates to be highly variable in southern Illinois and New York. Higher winter collision rates at single houses in these regions, compared to those reported elsewhere, are probably best explained by local site differences, the major one being the presence of feeding stations which attract large numbers of winter residents. Seedeaters predominated as strike casualties during the winter in both regions and included: Dark-eyed Junco, White-crowned (*Zonotrichia leucophrys*), and White-throated sparrow, and Northern Cardinal. Strikes in fall and spring consisted mainly of migrant warblers, thrushes, waxwings, and finches. Few birds hit windows in summer, probably because their movements are largely restricted to breeding territories. Southern Illinois species killed in summer were Ruby-throated Hummingbird (*Archilochus colubris*), fledgling White-eyed Vireo (*Vireo griseus*), Nashville Warbler (*Vermivora ruficapilla*, an early migrant), and Yellow-billed Cuckoo. The cuckoos were known breeders, determined by eggs in the oviduct. Although few in number, summer window-kills may result in the added loss of dependent eggs and young. Those species which occur in the greatest numbers during any one season will most likely comprise the greater number of window casualties for a particular site.

In Indiana, strike rates during daylight hours of sunrise to 13:00 were reported to be four times greater than at any other time of the day (Witzler et al. unpubl. data). In this study, most strikes occurred in early and late morning. Graber and Graber (unpubl. data) reported collisions throughout the daylight hours (06:0017:00) in southern Illinois, but more strikes occurred between 10:01-12:00 and 13:01-14:00 than at other times. At some localities strikes probably occur more often in early morning because birds are actively searching for food, and as most feeder watchers will testify, the largest concentration of birds at feeding stations usually occurs in early morning. Alternatively, during winter when large numbers of birds congregate at feeding stations, high strike rates can be expected throughout the day as local flocks periodically visit specific feeding stations.

Various weather conditions have been hypothesized to increase strikes by enhancing the deceptive effects of glass, hampering visibility, or accounting for the increased abundance of birds in the vicinity of manmade structures (Valum 1968, Konig 1963, Carpenter and Lovell 1963, Hall 1972). Most strikes occur under generally favorable weather, and probably are due to the clarity with which habitat is visible behind or reflected in glass. As my data further support, under conditions of poor visibility, during day or night, birds may experience spatial disorientation and become especially vulnerable if they descend to the vicinity of manmade structures and are attracted to lighted areas behind windows.

In summary, it is clear that: (1) birds fail to see windows as barriers and are vulnerable to them wherever they mutually occur, (2) any factor that increases the density of birds near windows will account for strike frequency, and (3) for any specific collision site, a combination of interacting factors must be considered to explain strike rates.

ACKNOWLEDGMENTS

I am indebted and grateful to W. G. George who introduced me to this study and further stimulated mv interest in and concern for man-caused wildlife mortality. For their comments and suggestions, I thank T. R. Anthoney, R. C. Banks, D. L. Beggs, C. R. Blem, W. G. Dyer, W. G. George, G. A. Hall, W. D. Klimstra, E. A. LeFebvre, R. Raible, B. Valum, and G. H. Waring. I thank M. and W. G. George, R. A. Klem, H. Schramm, M. Van Tuinen, and R. Vanderjack for help in the field. I am especially grateful to J. and M. Hayward, P. Rothstein, and several museum curators and individuals who collected or provided data, and to J. W. and R. R. Graber who gave me their unpublished manuscript to include in this paper. I thank A. T. Tax, H. Munch, and W. E. A. Reese for translations. Financial support or materials were given by W. G. George, The HugeCo. Inc., A. Mucci, Muhlenberg College, Pittsburgh Plate Glass Foundation, and Southern Illinois Univ. at Carbondale, Illinois. For their extensive support and interpretation I am most grateful to T. R. Anthoney, R. C. Banks, R. A. Klem, and A.-M. and G. H. Waring.

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SPACING AND ECOLOGY OF NORTH AMERICAN BADGERS (*TAXIDEA TAXUS*) IN A PRAIRIE-DOG (*CYNOMYS LEUCURUS*) COMPLEX

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We studied spacing, food habits, habitat use, and population characteristics of North American badgers (*Taxidea taxus*) in and around a prairie-dog (*Cynomys leucurus*) town in southeastern Wyoming, May 1991–October 1993. Densities of badgers varied from 0.8 to 1.1/km^2. Prairie dogs occurred in 57% of stomach and fecal samples from female badgers, and females used prairie dog towns more than expected from spatial availability of prairie-dog towns. Ninety-five percent adaptive–kernel home ranges of females were smaller than those of males (male $\bar{X} = 12.3 \pm 4.8$ km^2 [± *SD*], female $\bar{X} = 3.4 \pm 1.4$ km^2), and occurrence of overlap and geometric mean overlap were less for females than for males. Home ranges of males were larger during the breeding season than during the nonbreeding season (breeding $\bar{X} = 11.1 \pm 5.0$ km^2, nonbreeding $\bar{X} = 5.4 \pm 1.7$ km^2). Breeding home-range size of males was 2.5 times larger than that predicted (4.5 km^2) based on energetic demands. Spacing patterns of males were similar to those reported in other studies, but females were more territorial than reported elsewhere.

Key words: *Taxidea taxus,* North American badger, *Cynomys leucurus,* white-tailed prairie dog, territoriality, spacing patterns, Wyoming

Patterns of spatial use by mammals, often considered to infer social organization, have been the subject of detailed conceptual discussion and numerous empirical tests about optimization of use of space (Brown and Orians, 1970; Hixon, 1980, 1987; Lockie, 1966; Lott, 1991; Schoener, 1983; Waser and Wiley, 1979; Watson and Moss, 1970). For solitary carnivores, these studies have variously predicted (Powell, 1994; Sandell, 1989) and observed (Hornocker et al., 1983; Lockie, 1966; Minta, 1990, 1993) several important kinds of intraspecific variation in use of space: sexual, seasonal, and geographic. For example, black bears (*Ursus americanus*) and bobcats (*Lynx rufus*) maintain intrasexual territories in some areas (Bailey, 1974; Rogers, 1987) but not in others (Lindzey and Meslow, 1977; McCord and Cardoza, 1982).

Sexual and seasonal variations in size and overlap of home ranges generally have been attributed to differences in resources that hypothetically limit fitness, usually food for females and nonbreeding males, and fertile females for breeding males. For adult females, home-range size should be just large enough to include enough food to meet energetic requirements. For males during the breeding season, home-range size should reflect a strategy to maximize access to fertile females at this time. Hence, during the breeding season, the home range of a male in a polygynous mating system should be larger than that required to meet energetic demands (Frank and Heske, 1992; Lott, 1991; Minta, 1993; Powell, 1979; Sandell, 1989).

Several hypotheses have been proposed to account for geographic variation in spacing. Evenly distributed and temporally predictable resources (Brown and Orians, 1970; Hixon, 1980; Sandell, 1989), intermediate levels of prey availability (Carpenter and MacMillen, 1976; Powell, 1994), low intruder pressure (Hixon, 1980; Schoener, 1983), and low human-caused mortality (Hornocker et al., 1983) are believed to favor territoriality. These hypotheses tend not to exclude each other; for example, Minta (1993) argued that both patchily distributed food resources and high intruder pressure due to insularization of habitat resulted in high overlap of home ranges of female North American badgers (*Taxidea taxus*).

The North American badger provides a useful model of intrasexual and intraspecific variation in spatial use. It is sexually dimorphic and highly polygynous, so that predictions developed for typical solitary carnivores should apply. Also, its diet varies geographically, and prey species differ markedly in the patchiness of their distributions, which may influence spacing. The primary prey of badgers is the dominant burrowing rodent in an area, and in all previous studies with data on spacing patterns, this has been ground squirrels (*Spermophilus*) or smaller rodents (Lindzey, 1978, 1982; Messick and Hornocker, 1981; Messick et al., 1981; Minta, 1990, 1993). These studies reported a common spacing pattern: overlapping home ranges between and within sexes (Lindzey, 1978; Messick and Hornocker, 1981; Messick et al., 1981; Minta, 1990, 1993).

We studied badgers living on colonies of white-tailed prairie dogs (*Cynomys leucurus*) (Goodrich, 1994; Goodrich and Buskirk, 1995; Goodrich et al., 1994) because distribution and abundance of prairie dogs may differ from those of prey reported in other studies of badgers and therefore could influence spacing of females. Prairie-dog colonies, or towns, are often larger than home ranges of female badgers (Clark et al., 1982; Minta, 1993), so females can position their home ranges completely within a patch of prey where they should be more territorial than female badgers feeding on smaller patches of ground squirrels. Prairie dogs have been reported in only one previous study of diets of badgers (Bailey, 1931; Lampe, 1976, 1982; Lindzey, 1982; Messick, 1987; Minta, 1990), so we first determined diets of badgers at our study site.

We tested three predictions of the hypothesis that spacing patterns are determined by different factors for each sex (Frank and Heske, 1992; Lott, 1991; Minta, 1993; Powell, 1979; Sandell, 1989). First, home ranges of adult males during the breeding season should be larger than predicted based on metabolic demands. Second, home-range size of males should differ between breeding and nonbreeding seasons, with nonbreeding home-range size reflecting metabolic demands. Third, home ranges of females should be smaller and overlap less than those of males, a general pattern among Mustelidae (Powell, 1979) and reported before for North American badgers (Minta, 1993). We also examined differences between spacing of badgers on our study area and those reported in other studies. We predicted that if prairie dogs were the primary prey of female badgers on our study area, spacing of females would differ significantly (less home range overlap) from those reported in other studies that detected widely overlapping home ranges (Lindzey, 1978; Messick and Hornocker, 1981; Messick et al., 1981; Minta, 1993).

METHODS

Study area.—Our 28-km^2 study area was located in southeastern Wyoming (41°38′N, 106°20′W). Elevations ranged from 2,120 to 2,290 m above mean sea level, and topography consisted of flat areas, gently rolling hills, and some bluffs. Vegetation was the shrub-steppe typical of southeastern Wyoming (Knight, 1994). Most of the area was dominated by mixtures of Wyoming big sagebrush (*Artemesia tridentata wyomingensis*) and rabbit brush (*Chrysothamnus*), but curl-leaf mountain mahogany (*Cercocarpus montanus*) dominated bluffs. Grassy meadows and stands of greasewood (*Sarcobatus vermiculatus*) occurred around alkali lakes and most streams, except one stream that had a riparian area of herbaceous meadows and willow (*Salix*).

Capture and marking.—We caught badgers in padded leghold traps (Woodstream Softcatch™ Coyote Traps) or opportunistically with a net and noose pole from May to November 1991–1992. Traps were set near roads in the vicinity of fresh badger sign. We injected intramuscularly a 10:1 mixture of ketamine hydrochloride and xylazine hydrochloride (ca. 15 mg/kg body weight and 1.5 mg/kg, respectively) for anesthesia. Adult badgers ($n = 33$) were implanted with intraperitoneal transmitters (Telonics, Inc., Mesa, AZ and ATS, Isanti, MN).

Population estimates.—We used three different methods to estimate population size. First, we estimated population size of males ($N_{♂}$) using a Petersen estimate modified for sampling with replacement and Poisson confidence intervals for small samples (program PETERSEN; Krebs, 1989). We used transmitter-equipped adult male badgers captured in 1991 that were present on the study area as indicated by radio signals in 1992 ($n = 7$) as the marked sample and all non-target captures (animals captured without the aid of radiotelemetry) as the recapture sample ($n = 14$). We did not combine capture data for males and females because capture probabilities differed (Buskirk and Lindstedt, 1989; Messick and Hornocker, 1981; Minta, 1990). We could not estimate population size of adult females ($\mathrm{N}_{♀}$) by mark-recapture because of small samples ($n = 9$ in 1991 and 1992). Rather, we estimated $N_{♀}$ as $N_{♂}/1.3$, where 1.3 was the estimated ratio of males : females in our population (total adult population size, $N = N_{♂} + N_{♀}$. Because sex ratios of badgers may be male-skewed (Minta, 1990, 1993) and capture probabilities are as well, we used the midpoint between the sex ratio of adults in the 1991 capture sample (1:1.6, $n = 23$) and a 1:1 sex ratio. Second, we estimated $N_{♂}$ with a mark-recapture estimator (Minta and Mangel, 1989), using the same mark-recapture samples and method of estimating $\mathrm{N}_{♀}$ as described above. Third, we estimated density of adult females ($\rho_{♀}$) based on mean exclusive home-range size (HR_{E}) where $\mathrm{HR}_{\mathrm{E}} = \mathrm{HR}_{♀} - 2\bar{X}_0$, $\mathrm{HR}_{♀}$ was the mean 95% adaptive-kernel size of the home range of adult females, and $\bar{X}_0$ was the mean area of overlap of 95% adaptive-kernel contours of home range between adjacent pairs of adult females. We estimated population size of adult females ($N_{\mathrm{E}♀}$ where E referred to exclusive) from $\rho_{♀}$ by multiplying size of the area trapped by $\rho_{♀}$ and assuming that there were no vacant areas in the study area and each female home range was bordered by four other females. Male badgers did not have exclusive areas in their home ranges, so we estimated $N_{\mathrm{E}♂}$ as $1.3N_{\mathrm{E}♀}$ and the total adult population (N_{E}) as $N_{\mathrm{E}♂} + N_{\mathrm{E}♀}$.

Analysis of diets.—We estimated diets from three sources: feces collected from badgers held in captivity overnight in 1991, stomach contents of badgers killed in the study area in 1992, and stomach contents from badgers killed on the release site for black-footed ferrets (*Mustela nigripes*) in Shirley Basin, Wyoming, in 1991 and 1992. The release site for black-footed ferret was located ca. 50 km north of our study area and had similar vegetation and topography. We did not collect feces deposited on the ground because feces of badger and coyote are similar in appearance (Minta, 1990). Feces were washed in a 0.5-mm sieve, air dried, and spread over a 10-mm grid. Ten hair samples were taken from randomly selected grid cells, and casts were made as described by Moore et al. (1974), except that we used clear nail polish instead of polyvinyl-chloride sheets. Individual hairs and casts were identified to species by comparison with photographs in Moore et al. (1974) and with hairs taken from museum specimens. Most stomach contents consisted of easily identifiable mammal parts; otherwise we analyzed the contents as described for feces. Data were expressed as the percentage of samples that contained each food item. We compared the percentage of samples that contained prairie dogs between the two sites and sexes.

We compared use of prairie-dog towns by badgers with availability of prairie dog towns in the study area to determine if badgers preferred (use > availability) these areas. We mapped boundaries of prairie dog towns from the ground on 1:24,000 United States Geological Survey maps and estimated use of prairie dog towns by individual badgers as the proportion of telemetric locations of badgers that fell within town boundaries. We calculated mean use of prairie-dog towns by badgers at our site as the mean of individual use. We estimated availability of prairie dog towns as the percentage of the study area covered by prairie-dog towns.

Spacing.—Locations were collected from the ground by following a radio signal on foot until the badger was sighted or found in a burrow. We located badgers during all hours of the day and night but most often at night when animals were active and signals were easier to detect. Observers usually were within 50 m of an animal when it was located. We attempted to collect locations daily from May to November, and sampling was sporadic in winter. However, we often could not locate animals every day because signals did not carry far when animals were underground. We sampled most intensively during the breeding season ($\bar{X}$ = 1 location/6 days ± 4 *SD*; nonbreeding $\bar{X}$ = 1 location/17 days ± 9). Adaptive-kernel (Worton, 1989) and harmonic-mean (Dixon and Chapman, 1980) sizes of home range for six adult female and nine adult male badgers with ≥20 locations were estimated using CALHOME (Kie et al., 1994) for adaptive kernel and TELEM88 (Coleman and Jones, 1988) for harmonic mean. Harmonic-mean home ranges were used to compare with Minta (1990, 1993); adaptive-kernel home ranges were used for all other comparisons. Unless otherwise specified, home ranges are expressed as the 95% contour of the adaptive-kernel home range based on locations collected from both breeding (1 July–7 August) and non-breeding seasons. We used only locations collected from June 1991 through January 1992 and from April 1992 to October 1992 to analyze spacing because most badgers were removed from the study area during autumn 1992 (Goodrich, 1994).

To avoid serial autocorrelation, consecutive locations were separated by ≥24 h and at least one shift in activity as indicated by an animal's movements, which should result in independent locations (Lair, 1987; Minta, 1993) for a given animal. However, tests to determine independence of animal-movement data (Schoener, 1981; Swihart and Slade, 1985, 1986) indicated serial autocorrelation in some cases. Like Powell (1987), we disregarded serial autocorrelation because individual movements likely were dependent on past experience and knowledge of resources the home range.

To test the hypothesis that home ranges of female badgers would overlap less than those of males, we compared geometric mean overlap (Minta, 1992, 1993) between females and males and occurrence of intrasexual overlap between sexes. We assumed that occurrence of overlap increased linearly with increasing number of home ranges. We tested this assumption using a computer model that randomly filled an area the size of our study site with circles the size of the average home range for all badgers to examine the correlation between occurrence of overlap and number of home ranges.

We compared average home-range size between males and females and average home-range size of males between breeding and nonbreeding seasons. To test our prediction that the difference between home range size of males and females would be larger than that predicted from differences in body size and attributable to metabolic needs, we assumed that home ranges of females were set by metabolic demands and predicted home-range size of males (HR_{pred}) as $HR_{♀} \cdot M_{♂}/M_{♀}$, where M was mass (home-range size scaled linearly with body size; Lindstedt et al., 1986).

Statistics.—Means were compared with the Student's *t*-test, paired *t*-test, or Wilcoxon rank sum test (*Z*) (Ambrose and Ambrose, 1981). All other statistical comparisons were made with the *G*-test with Williams' adjustment (Sokal and Rohlf, 1981).

RESULTS

Density.—The two mark-recapture estimates of population size produced similar results (Table 1), whereas N_E was lower by 5–7 individuals. The latter estimate was about the same as the total number of badgers caught, which was a minimum population estimate.

Analysis of diets.—Adult female badgers were located on prairie-dog towns more often than were adult males (male $\bar{X}$ = 64% ± 21% *SD* of locations, female $\bar{X}$ = 88 ± 14%, $t = 3.01$, $d.f. = 25$, $P < 0.001$). Females used prairie-dog towns more than predicted from the spatial availability of prairie-dog towns (availability = 53%, $G = 8.64$, $d.f. = 1$, $P < 0.001$), but males did not ($G = 1.07$, $d.f. = 1$, $P = 0.3$). Five of the nine females were located only within prairie-dog towns.

The proportion of stomach and fecal samples of adult badgers that contained prairie dogs did not differ between our study area (55%, $n = 11$, where n is the total sample size) and the release site for

TABLE 1.—*Estimates of population size for adult badgers in southeastern Wyoming, 1992. Total population was estimated based on the number of males and a 1.3 sex ratio (M/F) for the two mark–recapture estimates and on the estimate of the number of females and a 1.3 sex ratio for* N_E *(parentheses enclose 95%* CI*).*

Category	Petersen–Poisson estimate	Minta–Mangel estimate	N_E	Number caught
Males	16 (14–21)	17 (14–24)	13	14
Females	12 (11–16)	13 (11–18)	10	9
Total	28 (25–37)	30 (25–42)	23	23
Density (N/km^2)	1 (0.9–1.3)	1.1 (0.9–1.5)	0.8	0.8

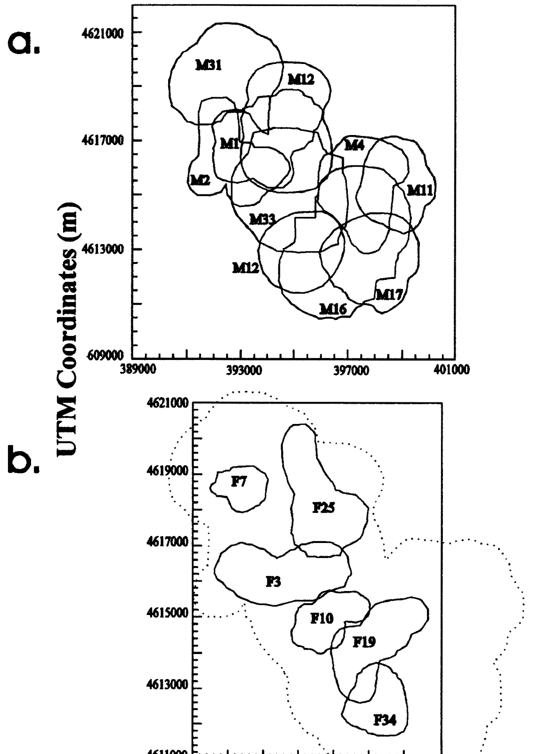

FIG. 1.—Overlap of 95% adaptive-kernel home ranges of a) nine adult male badgers and b) six adult female badgers in southeastern Wyoming, 1991–1992. Dotted line is a tracing of the outermost home range boundaries of all males to illustrate the relationship between home ranges of males and females (scale is larger for the plot of home ranges of females; axes present universal transverse mercator, UTM, coordinates).

black-footed ferrets (52%, $n = 33$; $G = 0.01$, *d.f.* = 1, $P = 0.91$), so data from the two sites were combined. Of 44 stomach and fecal samples examined, 52% contained white-tailed prairie dogs, 29% contained ground squirrels, 20% contained cottontail rabbits (*Sylvilagus audubonii*), 9% contained voles (*Microtus*), 7% contained unidentifiable vertebrate remains, 2% contained deer mice (*Peromyscus maniculatus*), and 2% contained white-tailed jack rabbits (*Lepus townsendii*). The proportion of samples that contained prairie dogs did not differ between adult males and adult females (males = 50%, $n = 30$, females = 57%, $n = 14$; $G = 0.09$, *d.f.* = 1, $P = 0.76$). There was no difference between the proportion of samples that contained prairie dogs and the next most common food item, ground squirrels, for males (30%; $G = 0.99$, *d.f.* = 1, $P = 0.32$) or females (21%; $G = 2.36$, *d.f.* = 1, $P = 0.13$).

Spacing.—Annual 95% adaptive-kernel size of home range of nine males was larger than that of six females (male $\bar{X} = 12.3 \pm 4.8$ km^2, females $\bar{X} = 3.4 \pm 1.4$ km^2, $t = 4.4$, *d.f.* = 13, $P < 0.001$). Median geometric mean overlap of 95% home-range contours was greater among males ($n = 21$) than females ($n = 4$) (male = 0.20 ± 1.86, female = 0.08 ± 0.06, $Z = -1.82$, $P = 0.03$). Male–male overlap was more frequent than female-female overlap (Fig. 1); there were 21 overlapping pairs among the nine male badgers and four overlapping pairs among the six female badgers ($G = 6.67$, *d.f.* = 1, $P = 0.01$). Occurrence of overlap increased linearly with increasing number of home ranges ($r^2 = 0.96$, *d.f.* = 23, $P < 0.001$), satisfying an assumption of the test. To test for sexual differences in spacing, we examined average distance between home-range centers (geometric mean of all locations) by sex, using all possible pairs of home ranges. Spacing of males did not differ from that of females (male $\bar{X}$ = 3.9 ± 1.9 km, female $\bar{X}$ = 3.5 ± 1.7 km, $t = -0.76$, *d.f.* = 49, $P = 0.22$). Given that sex ratio was equal or male-skewed and home ranges of males were larger than those of females, home ranges of males had to overlap more.

Home-range size of males in the breeding season ($\bar{X}$ = 11.1 km^2) was 2.5 times greater than predicted (4.5 km^2) based on body size ($t = 3.5$, *d.f.* = 6, $P = 0.006$), but home-range size of males in the nonbreeding season was not different from our prediction ($\bar{X}$ = 5.4 ± 1.7 km^2, $t = 1.4$, *d.f.* = 6, $P = 0.11$). Home-range size of males was greater in the breeding season ($\bar{X}$ = 11.1 ± 5.0 km^2, nonbreeding $\bar{X}$ = 5.4 ± 1.7 km^2, $t = 2.6$, *d.f.* = 6, $P = 0.02$). Two of the nine males were excluded from this analysis because we located them <10 times during the breeding season. For the seven males tested, number of locations were smaller for home ranges during the breeding season ($\bar{X}$ = 16.7 ± 6.7, nonbreeding $\bar{X}$ = 30.1 ± 17.0, $t = 1.9$, *d.f.* = 12, $P = 0.038$), which made our test conservative because small samples tend to underestimate home-range size (Bekoff and Mech, 1984).

DISCUSSION

Prairie dogs were found in twice as many stomachs and feces of badgers than were ground squirrels, although this difference did not differ significantly in our small samples. Also, adult female badgers occupied prairie-dog towns more than predicted from the spatial extent of the towns. Therefore, we conclude that badgers on our study area ate primarily prairie dogs.

Male badgers had larger and less exclusive home ranges than females, annual home ranges of males were larger than predicted based on energetic demands, and home ranges of males were larger in the breeding season than the nonbreeding season. The latter two findings support the assumption that fertilizable females are a critical resource determining home-range size for males during the breeding season. Home-range size of males in the nonbreeding season ($\bar{X}$ = 5.4 km^2) was not significantly larger than that predicted based on energetic demands (4.5 km^2), indicating that males set home-range size in the same way as do females in the nonbreeding season.

Minta (1990, 1993) also found high overlap among home ranges of males, which he attributed to large home ranges, high intruder pressure from males, and spatial and temporal variability of fertilizable females. Costs of defending a large home range include energy to patrol a long boundary (Hixon, 1980; Schoener, 1983) and, perhaps more importantly, lost opportunity to search for estrous females. Intruder pressure from other adult males likely was high because the operational sex ratio (ratio of fertilizable females to sexually active males; Emlen and Oring, 1977) is strongly male-skewed in badgers because estrus is brief and asynchronous. Thus, few females are ready to mate at any one time, while most males are. Short asynchronous estrus in highly mobile females results in fertilizable females being a resource that is spatially and temporally unpredictable (Minta, 1993). All of these characteristics should lead to widely overlapping home ranges (Frank and Heske, 1992; Lott, 1991; Minta, 1993; Powell, 1979; Sandell, 1989; Waser and Wiley, 1979).

Home ranges of females overlapped very little; all previous studies have found high overlap among females (Hornocker et al., 1983; Lindzey, 1978; Messick and Hornocker, 1981; Minta, 1993), but Minta (1993) was the only one who quantified overlap. Geometric mean overlap (ca. 0.2) of 95% harmonic mean home ranges of females on his study area was twice as high as that on our study area (0.08 for adaptive kernel and 0.1 for harmonic mean), despite small home ranges on his study site ($\bar{X} = 2.8$ km^2 for 95% harmonic mean). These findings support our prediction that female badgers on our study site would space themselves differently from those elsewhere.

That home ranges of females on our study site were larger with less overlap than those in other studies contradicts Sandell's (1989) prediction that exclusive home ranges should be smaller than overlapping ones. However, that prediction is not valid if intermediate levels of prey availability favor territoriality (Carpenter, 1987; Carpenter and MacMillen, 1976; Powell, 1994) and home-range size is correlated with available prey biomass (Powell, 1994; Sandell, 1989); high prey availability should favor both small home ranges and high overlap.

Factors that favor territoriality among female solitary carnivores include food that is evenly distributed, stable over time, and intermediate in availability (Brown and Orians, 1970; Carpenter and MacMillen, 1976; Hixon, 1980; Powell, 1994; Sandell, 1989; Waser and Wiley, 1979). Data on biomass and vulnerability of prey to badger predation are not available for comparisons among studies, but sufficient information is available for speculative comparisons regarding distribution and stability of prey. We believe that prairie dogs constituted an evenly distributed resource for badgers relative to ground squirrels, which were the primary resource in most earlier studies of home-range overlap (Messick et al., 1981; Messick and Hornocker, 1981; Minta, 1993). Both Minta (1990) and Messick and Hornocker (1981) reported considerable variability in densities of ground squirrel among habitats, including habitats without ground squirrels. In contrast, our study area was dominated by two prairie-dog towns that were large enough (9 km^2 and 22 km^2) that several female badgers positioned their home ranges within town boundaries. Hence, most females had prairie dogs available in one large patch throughout their home ranges.

Availability of prairie dogs also was probably more predictable than that of ground squirrels over time. Access to ground squirrels by badgers in other studies varied seasonally because ground squirrels hibernated and aestivated (Messick and Hornocker, 1981), and deep snow hindered ability of badgers to hunt ground squirrels (Minta, 1990). In contrast, prairie dogs on our study site were active from April through November, and we occasionally observed them above ground in winter. Likewise, high winds swept most of our study area clear of snow. Anecdotal radio- and snow-tracking data collected in December 1991 and January 1992 indicated that badgers preyed on prairie dogs in winter. Thus, we believe that prairie dogs represented a more stable resource to badgers than did ground squirrels in other studies, which promoted territoriality.

In other studies, several factors led to high intruder pressure among females and hence increased home-range overlap, including insularization of habitat that inhibited dispersal (Minta, 1990), high densities of badgers and a population crash of prey (Messick and Hornocker, 1981), and high human-caused mortality (Hornocker et al., 1983). In contrast, density on our site was relatively low; the study area was contiguous with large areas of habitat for badgers, and human-caused mortality not related to our study was low (Goodrich, 1994), so intruder pressure among females was probably low.

Spacing patterns of badgers varied between sexes, between seasons, and geographically. Sexual and seasonal variation reflected differences in factors most important to individual fitness: food for females and nonbreeding males and fertilizable females for breeding males. Geographical variation in spacing patterns of females was probably due to differences in distribution and abundance of food.

ACKNOWLEDGMENTS

This project was funded by the United States Fish and Wildlife Service, United States Bureau of Land Management, National Fish and Wildlife Foundation, Wyoming Game and Fish Department, and Chevron USA. The Wyoming Game and Fish Department and the United States Fish and Wildlife Service also provided field vehicles. H. Harju, H. Harlow, F. Lindzey, E. Williams, D. Biggins, R. Luce, and S. Minta provided advice on study design and logistics. E. Williams and H. Harlow advised and assisted with surgical techniques. L. Kerley, A. Vargas, H. Harju, H. Harlow, F. Lindzey, S. Minta, E. Williams, and two anonymous reviewers provided helpful comments on previous drafts. L. Oberhofer, W. Cook, B. Pierce, T. Woolley, M. Peacock, L. Woolley, T. Goodrich, D. Hoff, L. Kerley, M. Secord, K. Clark, and S. Taylor assisted with collection of data.

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Submitted 24 February 1996. Accepted 10 March 1997.

Associate Editor was Edward J. Heske.

Viewsheds: a complementary management approach to buffer zones

Richard J. Camp, David T. Sinton, and Richard L. Knight

Recreational activities may displace and disturb wildlife, as well as contribute to wildlife mortality (Knight and Gutzwiller 1995). Management actions currently used to reduce harmful effects of human activities are based on activity or access restrictions (Knight and Temple 1995). Land managers typically identify a species sensitive to disturbance, such as a bird-of-prey, and during sensitive periods (e.g., reproduction) create a spatial buffer zone within which human activities are restricted (Knight and Skagen 1988).

Wildlife may be disturbed prior to actual flight. McGarigal et al. (1991) developed the Dual Disturbance Threshold Model which categorized wildlife responses to disturbance at *agitation* and *flushing* distances (also see Anthony et al. 1995). This model acknowledges that wildlife respond to disturbances physiologically before they respond behaviorally. Heart rate increases and attention is diverted to human activities at a distance greater (the *agitation* point) than the distance where wildlife actually flee (the *flushing* distance). Spatial buffer zones, however, are implemented at the flushing distance.

The Nature Conservancy at Phantom Canyon Preserve, Colorado, regulates visitors and their activities but allows guided field trips, fishing, and work parties. Within the preserve are 2 occupied golden eagle (*Aquila chrysaetos*) territories. Given the importance of cliffs to nesting raptors and the relative lack of understanding of the effects of human activities on wildlife, we surveyed the cliff habitat used by nesting golden eagles at this preserve. Subsequently, using both a geographic information system (GIS) and a global positioning system (GPS), we developed a management scheme that considered spatial zones incorporating the viewshed from each nest. We defined a viewshed as the area visible across a landscape from a point location (nest site).

Methods

The Nature Conservancy's Phantom Canyon Preserve is located in Larimer County, Colorado, 40°N, 105°E, and comprises approximately 470 ha, including 8.5 km of the North Fork of the Cache la Poudre River. In addition, a contiguous 220-ha area and 1.5 km of the river form a conservation easement managed by The Nature Conservancy and considered part of the Phantom Canyon Preserve. The river bisects Phantom Canyon Preserve through the surrounding short grass prairie and foothills of the Rocky Mountains to form a canyon (approx 150 m below the rim).

Between 31 January and 26 February 1994, we searched all cliffs in the Phantom Canyon Preserve (including the Conservation Easement) for eagle nests. We found 6 nests and measured nest exposure and nest-site characteristics by rappelling into each nest. We determined the location of each nest using a GPS. The GPS used was the Trimble Scout (Trimble Navigation 1992, 1994). At each point, 3-dimensional fixes were obtained; however, due to the topography of the canyon, 2-dimensional fixes were used in some cases. The GPS was configured to register spatial data in North American Datum of 1927, a projection of UTMs and elevation in meters.

We digitized the boundary of the Phantom Canyon Preserve. Next we entered the cliff periphery points and eagle nest sites into Arc/Info, Version 6.1 (ESRI 1991) on a Sun Sparc workstation (Sun Microsystem, Mountain View, Calif.). For cliffs, arcs were added connecting the corners, thus creating cliff polygons.

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Key words: *Aquila chrysaetos*, buffer zone, Colorado, disturbance management, geographic information systems, golden eagle, viewshed

Wildlife Society Bulletin 1997, 25(3):612–615 **Peer edited**

Nest and cliff coverages were based on field data that were spatially corrected. We used the Livermore Mountain Digital Elevation Model (DEM; U.S. Geol. Surv., electronic data, 1993), which contains the entire Phantom Canyon Preserve, for this project. For consistency each of the coverages was created or converted to the North American Datum of 1927, UTM-zone 13 projection in meters.

A buffer zone of a 333-m radius has been suggested for golden eagle nests when the birds are rearing young and exposed to a variety of human activities (Suter and Joness 1981). Accordingly, for each nest we generated a spatial buffer zone of a 333-m radius using Arc/Info (BUFFER algorithm, ESRI 1991). Arc/Info (VISIBILITY algorithm, ESRI 1991) and the DEM were used to generate the viewshed cover. No portion of the DEM was visible beyond a 3-km radius of a nest because nests were below the canyon rim. Therefore, we restricted each viewshed algorithm to sample for visible portions within a 3-km radius from each nest. This included lands within the preserve as well as private lands adjacent to the preserve. Buffer zones and viewsheds for each eagle nest were overlaid on a map of Phantom Canyon Preserve and the surrounding private lands.

Results

The total area that fell within the 333-m-radius buffer zones was 145 ha, while the area encompassed by the viewsheds was 434 ha (Fig. 1). One nest was located several meters above another; therefore, the projections overlaid each other and only 5 nest sites are apparent in Figure 1. The total area included within the 333-m-radius buffer zones that fell within Phantom Canyon Preserve and the private lands was 133 and 12 ha, respectively. The total area within the viewsheds that fell within Phantom Canyon Preserve and the private lands was 278 and 156 ha, respectively. Collectively, buffer zones and viewsheds comprised 48% (330 ha) of the Phantom Canyon Preserve, and 168 ha extended onto private land.

Discussion

Cliffs concentrate a unique group of biologically diverse species, including raptors (Camp and Knight 1997). A variety of raptor species are either obligate cliff nesters or nearly so (Newton 1979). The wild-

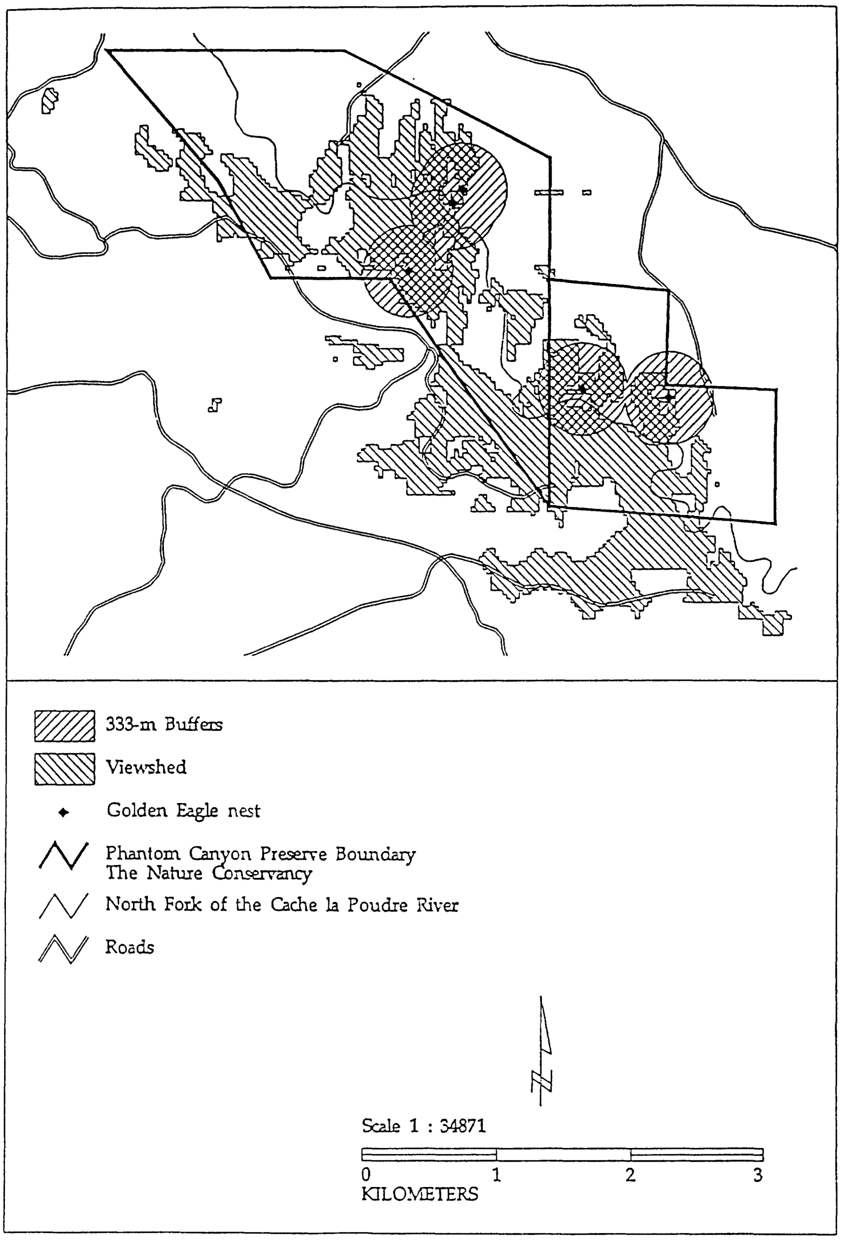

Fig. 1. Viewshed and buffer zones for golden eagle nests in Phantom Canyon, Colorado, 1994. One nest was located several meters above another; therefore, only 5 nests are apparent in the figure.

life-viewing public seeks out cliffs specifically to observe raptors and expects land managers to preserve these species. The viewsheds from all of the nests and 2 of the buffer zones in the Phantom Canyon Preserve fell outside the preserve boundary. Within the preserve, access to the river from the canyon rim is restricted to 1 trail, which descends through an eagle viewshed. Visitors at the river continue to be within sight of nesting birds as the viewsheds overlap and include most of the canyon floor.

Proactive management plans can be developed to minimize human activities potentially disturbing to eagles. If breeding eagles are flushed from the nest, eggs or young may experience adverse temperature changes and predation. Disturbance may also disrupt feeding of the young and result in increased nestling mortality (Knight and Skagen 1988). Viewshed management provides a more accurate assessment of birds' needs at individual nests. When birds are shielded from disturbances by vegetation (Stalmaster and Newman 1978) or topographical features such as cliffs, flushing distances are reduced. The use of viewsheds provides a manager with a realistic understanding of spatial requirements. Indeed, a viewshed approach to spatially managing disturbance may require less protected area than buffer zones, although this was not the case in our study.

We suggest that a more comprehensive approach to protecting wildlife from disturbance may include both a buffer zone and a viewshed. This dual approach may restrict activities potentially harmful to birds within the buffer zone, or flushing area, as well as mitigating wildlife responses to activities within the viewshed, or agitation area (McGarigal et al. 1991, Anthony et al. 1995). By creating viewsheds for sensitive species, managers may be better able to locate trails, panoramic sites, and tours, so as to minimize disturbances from these kinds of activities and regulate human activities during specific seasons. In addition, a viewshed database is dynamic in response to changes in wildlife distribution and proposed land-use projects. Newly located as well as recently inactive wildlife sites and proposed management activities can be incorporated into the existing database to assess potential impacts on wildlife.

Acknowledgments. We thank D. Dean for GIS technical support, and G. Janson for GPS equipment and technical support. M. Siders and L. Metz provided additional support. H. A. L. Knight provided helpful comments on this manuscript. This project was supported by the City of Thorton, Colorado, in conjunction with the Colorado Office of The Nature Conservancy and Colorado State University.

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Richard (Rick) J. Camp (left) received his M.S. from Colorado State University. He is interested in the response of wildlife communities to human disturbances, and the foraging ecology of predatory birds in American deserts. ***David T. Sinton*** is a wildlife biologist at the North Kaibab Ranger District, U.S. Forest Service. He received his B.S.F from Northern Arizona University. He currently studies human disturbances on northern goshawks. ***Richard (Rick) L. Knight*** (right) is a professor of wildlife conservation at Colorado State University. He received his Ph.D. from the University of Wisconsin-Madison. His service and research interests deal with land-use practices on both private and public lands in the American West. With Curt Meine, he is editing a book for the University of Wisconsin Press called *The Essence of Aldo Leopold.*

Application No:	A.08-03-015
Exhibit No.	SCE-3
Witnesses:	B. Hodges D. Klun D. Snow

SOUTHERN CALIFORNIA
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(U 338-E)

Solar Photovoltaic (PV) Program
Supplemental Rebuttal Testimony

Before the

Public Utilities Commission of the State of California

October 14, 2008
Rosemead, California

Solar Photovoltaic (PV) Program
Supplemental Rebuttal Testimony

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I.

DESCRIPTION OF EXTENSION OF INVESTMENT TAX CREDITS (ITCs) TO UTILITY-OWNED SOLAR PV SYSTEMS IN GOVERNMENT REVENUE PLAN

On Friday October 3, 2008, the President signed into law the Emergency Economic Stabilization Act of 2008 (H.R.1424). The Energy Production Incentives section of this newly enacted law, specifically Act Section 103 Energy Credit, made two important tax law changes which impact the tax rules applicable to the Solar Property included in this filing. A copy of that Act section is included in Appendix A.

First, Act Section 103(a), extended the period for which the 30% Solar Energy Credit may be claimed. The credit, which had formerly been scheduled to expire on December 31, 2008, is now extended through December 31, 2016. Second, Act Section 103(e) removed the language in Internal Revenue Code section 48, which had previously precluded public utilities from claiming the credit.

Southern California Edison Company (SCE) is filing this supplemental testimony to reflect these tax law changes. As indicated in Exhibit SCE-1 revised, SCE intended to pass through to ratepayers all tax benefits to which it is entitled, if the solar credit legislation was enacted. As a result, SCE now claims the 30% Solar Investment Tax Credit on the eligible property. This credit is passed through to ratepayers ratably over the book life of the property following SCE's election under section 46(f)(2) of the Internal Revenue Code. SCE has also reduced the tax basis of the property by 50% of the credit claimed following Internal Revenue Code section 50(c)(3)(A). California tax computations remain unchanged, as there is no conforming legislation.

Chapter II contains New Revenue Requirement computations which reflect these changes.

II.

EFFECT OF ITCs ON REVENUE REQUIREMENT CALCULATION

This chapter provides the impact of the recently enacted Emergency Economic Stabilization Act of 2008 on SCE's estimated Solar PV Program revenue requirement consistent with Chapter I above. Table V-10 in Exhibit SCE-1 (revised) sets forth the estimated annual Solar PV Program revenue requirements for the period 2008 through 2014.[1] Table II-1 below shows the updated estimated annual Solar PV Program revenue requirements for the same period including the new ITC provisions contained in the new legislation. In addition, Table II-1 shows that the reduction in the estimated Solar PV Program revenue requirement over this seven-year period from SCE's previous estimate is $61.7 million.

Table II-1
Revised Estimated Annual Solar PV Program Revenue Requirements
As The Result of New Investment Tax Credit Provisions

Line No.	Item	2008 1/	2009	2010	2011	2012	2013	2014	Total	Previous Rev Rqmt 2/	Change
1.	**Operating Revenues**	**2,923**	**22,012**	**52,710**	**81,163**	**107,251**	**130,573**	**135,956**	**532,588**	**594,285**	**(61,697)**
2.	**Operating Expenses:**										
3.	O&M Expense	877	2,911	4,586	6,252	8,013	9,713	10,005	42,358	42,358	0
4.	A&G - benefits	298	536	596	614	632	651	671	3,999	3,999	0
5.	Uncollectible Expense	7	50	119	183	241	294	306	1,198	1,337	(139)
6.	Franchise Requirements	26	197	471	725	958	1,166	1,214	4,757	5,307	(550)
7.	Depreciation	504	6,207	15,713	25,412	35,322	44,939	49,375	177,473	177,473	(0)
8.	Taxes Other than Income	0	120	1,203	3,012	4,626	6,103	7,363	22,427	21,746	681
9.	Taxes Based on Income	381	1,747	4,380	5,714	5,824	5,514	4,342	27,900	97,239	(69,339)
10.	Total Operating Expenses	2,093	11,768	27,067	41,911	55,616	68,380	73,277	280,112	349,459	(69,347)
11.	**Net Operating Revenue**	**830**	**10,244**	**25,643**	**39,252**	**51,635**	**62,193**	**62,679**	**252,476**	**244,826**	**7,650**
12.	**Rate Base (Average)**	8,501	105,062	263,010	402,584	529,593	637,873	642,865	2,589,488	2,511,017	78,471
13.	**Rate of Return**	9.75%	9.75%	9.75%	9.75%	9.75%	9.75%	9.75%	9.75%	9.75%	9.75%

1/ The 2008 annual revenue requirement has been prorated assuming an effective date of April 1, 2008.
2/ As filed on May 14, 2008

---

[1] As filed on May 14, 2008.

III.

EFFECT OF ITCs ON ¢/KWH COST OF SOLAR PV PROGRAM

SCE's ability to claim the ITCs reduces the cost of Solar PV Program to ratepayers. While SCE proposes to recover the Solar PV Program costs under traditional ratemaking as forecast in the previous section, this Chapter provides a calculation of the $/kWh on a levelized basis with and without an estimated Time of Day (TOD) adjustment[2]. The ITC benefit reduces the levelized cost of Solar PV Program to $0.27/kWh ($0.19/kWh with TOD adjustment). Figure III-1 below compares traditional ratemaking cost with the levelized costs. As discussed in Exhibit SCE-2, Chapter II.B, the Commission has determined that utility-owned generation and Power Purchase Agreement are not directly comparable.[3] As such, this is not as a Renewable Portfolio Standard (RPS) equivalent number even with the TOD adjustment.

---

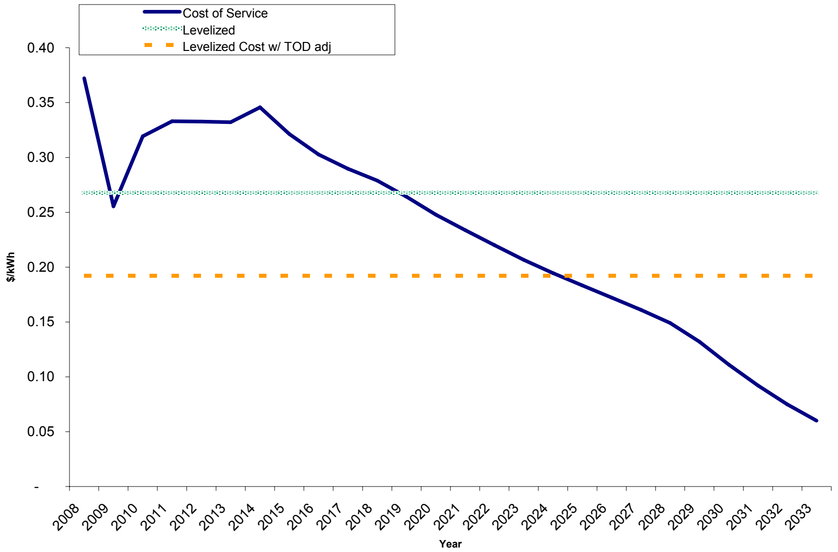
[2] ToD adjustment estimate calculated as weighted average of (512 summer – on hours at 3.13, 768 summer – mid at 1.35, and 2,189 winter – mid hours at 1.00) = 1.39

[3] SCE Solar PV Program Rebuttal

Figure III-1

Solar PV Program

Revenue Requirement ($/kWh)



Appendix A

Emergency Economic Stabilization Act of 2008, Section 103(a)

the date of the enactment of this Act, in taxable years ending after such date.

SEC. 103. ENERGY CREDIT.

(a) EXTENSION OF CREDIT.—

(1) SOLAR ENERGY PROPERTY.—Paragraphs (2)(A)(i)(II) and (3)(A)(ii) of section 48(a) are each amended by striking "January 1, 2009" and inserting "January 1, 2017".

(2) FUEL CELL PROPERTY.—Subparagraph (E) of section 48(c)(1) is amended by striking "December 31, 2008" and inserting "December 31, 2016".

(3) MICROTURBINE PROPERTY.—Subparagraph (E) of section 48(c)(2) is amended by striking "December 31, 2008" and inserting "December 31, 2016".

(b) ALLOWANCE OF ENERGY CREDIT AGAINST ALTERNATIVE MINIMUM TAX.—

(1) IN GENERAL.—Subparagraph (B) of section 38(c)(4), as amended by the Housing Assistance Tax Act of 2008, is amended by redesignating clause (vi) as clause (vi) and (vii), respectively, and by inserting after clause (iv) the following new clause:

"(v) the credit determined under section 46 to the extent that such credit is attributable to the energy credit determined under section 48,".

(2) TECHNICAL AMENDMENT.—Clause (vi) of section 38(c)(4)(B), as redesignated by paragraph (1), is amended by striking "section 47 to the extent attributable to" and inserting "section 46 to the extent that such credit is attributable to the rehabilitation credit under section 47, but only with respect to".

(c) ENERGY CREDIT FOR COMBINED HEAT AND POWER SYSTEM PROPERTY.—

(1) IN GENERAL.—Section 48(a)(3)(A) is amended by striking "or" at the end of clause (iii), by inserting "or" at the end of clause (iv), and by adding at the end the following new clause:

"(v) combined heat and power system property,".

(2) COMBINED HEAT AND POWER SYSTEM PROPERTY.—Subsection (c) of section 48 is amended—

(A) by striking "QUALIFIED FUEL CELL PROPERTY; QUALIFIED MICROTURBINE PROPERTY" in the heading and inserting "DEFINITIONS", and

(B) by adding at the end the following new paragraph:

"(3) COMBINED HEAT AND POWER SYSTEM PROPERTY.—

"(A) COMBINED HEAT AND POWER SYSTEM PROPERTY.—The term 'combined heat and power system property' means property comprising a system—

"(i) which uses the same energy source for the simultaneous or sequential generation of electrical power, mechanical shaft power, or both, in combination with the generation of steam or other forms of useful thermal energy (including heating and cooling applications),

"(ii) which produces—

"(I) at least 20 percent of its total useful energy in the form of thermal energy which is not used to produce electrical or mechanical power (or combination thereof), and

"(II) at least 20 percent of its total useful energy in the form of electrical or mechanical power (or combination thereof),

"(iii) the energy efficiency percentage of which exceeds 60 percent, and

"(iv) which is placed in service before January 1, 2017.

"(B) LIMITATION.—

"(i) IN GENERAL.—In the case of combined heat and power system property with an electrical capacity in excess of the applicable capacity placed in service during the taxable year, the credit under subsection (a)(1) (determined without regard to this paragraph) for such year shall be equal to the amount which bears the same ratio to such credit as the applicable capacity bears to the capacity of such property.

"(ii) APPLICABLE CAPACITY.—For purposes of clause (i), the term 'applicable capacity' means 15 megawatts or a mechanical energy capacity of more than 20,000 horsepower or an equivalent combination of electrical and mechanical energy capacities.

"(iii) MAXIMUM CAPACITY.—The term 'combined heat and power system property' shall not include any property comprising a system if such system has a capacity in excess of 50 megawatts or a mechanical energy capacity in excess of 67,000 horsepower *or an equivalent combination of electrical and mechanical energy capacities.*

"(C) SPECIAL RULES.—

"(i) ENERGY EFFICIENCY PERCENTAGE.—For purposes of this paragraph, the energy efficiency percentage of a system is the fraction—

"(I) the numerator of which is the total useful electrical, thermal, and mechanical power produced by the system at normal operating rates, and expected to be consumed in its normal application, and

"(II) the denominator of which is the lower heating value of the fuel sources for the system.

"(ii) DETERMINATIONS MADE ON BTU BASIS.—The energy efficiency percentage and the percentages under subparagraph (A)(ii) shall be determined on a Btu basis.

"(iii) INPUT AND OUTPUT PROPERTY NOT INCLUDED.—The term 'combined heat and power system property' does not include property used to transport the energy

source to the facility or to distribute energy produced by the facility.

"(D) SYSTEMS USING BIOMASS.—If a system is designed to use biomass (within the meaning of paragraphs (2) and (3) of section 45(c) without regard to the last sentence of paragraph (3)(A)) for at least 90 percent of the energy source—

"(i) subparagraph (A)(iii) shall not apply, but

"(ii) the amount of credit determined under subsection (a) with respect to such system shall not exceed the amount which bears the same ratio to such amount of credit (determined without regard to this subparagraph) as the energy efficiency percentage of such system bears to 60 percent.".

(3) CONFORMING AMENDMENT.—Section 48(a)(1) is amended by striking "paragraphs (1)(B) and (2)(B)" and inserting "paragraphs (1)(B), (2)(B), and (3)(B)".

(d) INCREASE OF CREDIT LIMITATION FOR FUEL CELL PROPERTY.—Subparagraph (B) of section 48(c)(1) is amended by striking "$500" and inserting "$1,500".

(e) PUBLIC UTILITY PROPERTY TAKEN INTO ACCOUNT.—

(1) IN GENERAL.—Paragraph (3) of section 48(a) is amended by striking the second sentence thereof.

(2) CONFORMING AMENDMENTS.—

(A) Paragraph (1) of section 48(c) is amended by striking subparagraph (D) and redesignating subparagraph (E) as subparagraph (D).

(B) Paragraph (2) of section 48(c) is amended by striking subparagraph (D) and redesignating subparagraph (E) as subparagraph (D).

(f) EFFECTIVE DATE.—

(1) IN GENERAL.—Except as otherwise provided in this subsection, the amendments made by this section shall take effect on the date of the enactment of this Act.

(2) ALLOWANCE AGAINST ALTERNATIVE MINIMUM TAX.—The amendments made by subsection (b) shall apply to credits determined under section 46 of the Internal Revenue Code of 1986 in taxable years beginning after the date of the enactment of this Act and to carrybacks of such credits.

(3) COMBINED HEAT AND POWER AND FUEL CELL PROPERTY.—The amendments made by subsections (c) and (d) shall apply to periods after the date of the enactment of this Act, in taxable years ending after such date, under rules similar to the rules of section 48(m) of the Internal Revenue Code of 1986 (as in effect on the day before the date of the enactment of the Revenue Reconciliation Act of 1990).

(4) PUBLIC UTILITY PROPERTY.—The amendments made by subsection (e) shall apply to periods after February 13, 2008, in taxable years ending after such date, under rules similar to the rules of section 48(m) of the Internal Revenue Code of 1986 (as in effect on the day before the date of the enactment of the Revenue Reconciliation Act of 1990).

SEC. 104. ENERGY CREDIT FOR SMALL WIND PROPERTY.

(a) IN GENERAL.—Section 48(a)(3)(A), as amended by section 103, is amended by striking "or" at the end of clause (iv), by adding "or" at the end of clause (v), and by inserting after clause (v) the following new clause:

"(vi) qualified small wind energy property,".

(b) 30 PERCENT CREDIT.—Section 48(a)(2)(A)(i) is amended by striking "and" at the end of subclause (II) and

Bill Powers

From: Don Kondoleon [Dkondole@energy.state.ca.us]

Sent: Wednesday, January 30, 2008 3:05 PM

To: Bill Powers

Cc: Matthew Layton

Subject: Re: average and peak T&D losses

Bill--- I checked with my staff and unfortunately we do not have a report that documents the loss figures in question. However, they do believe that the 7.5% loss figure on an annual average basis and the 14% loss figure on peak are reasonable assumptions. Sorry I could not be of more help.

Don.

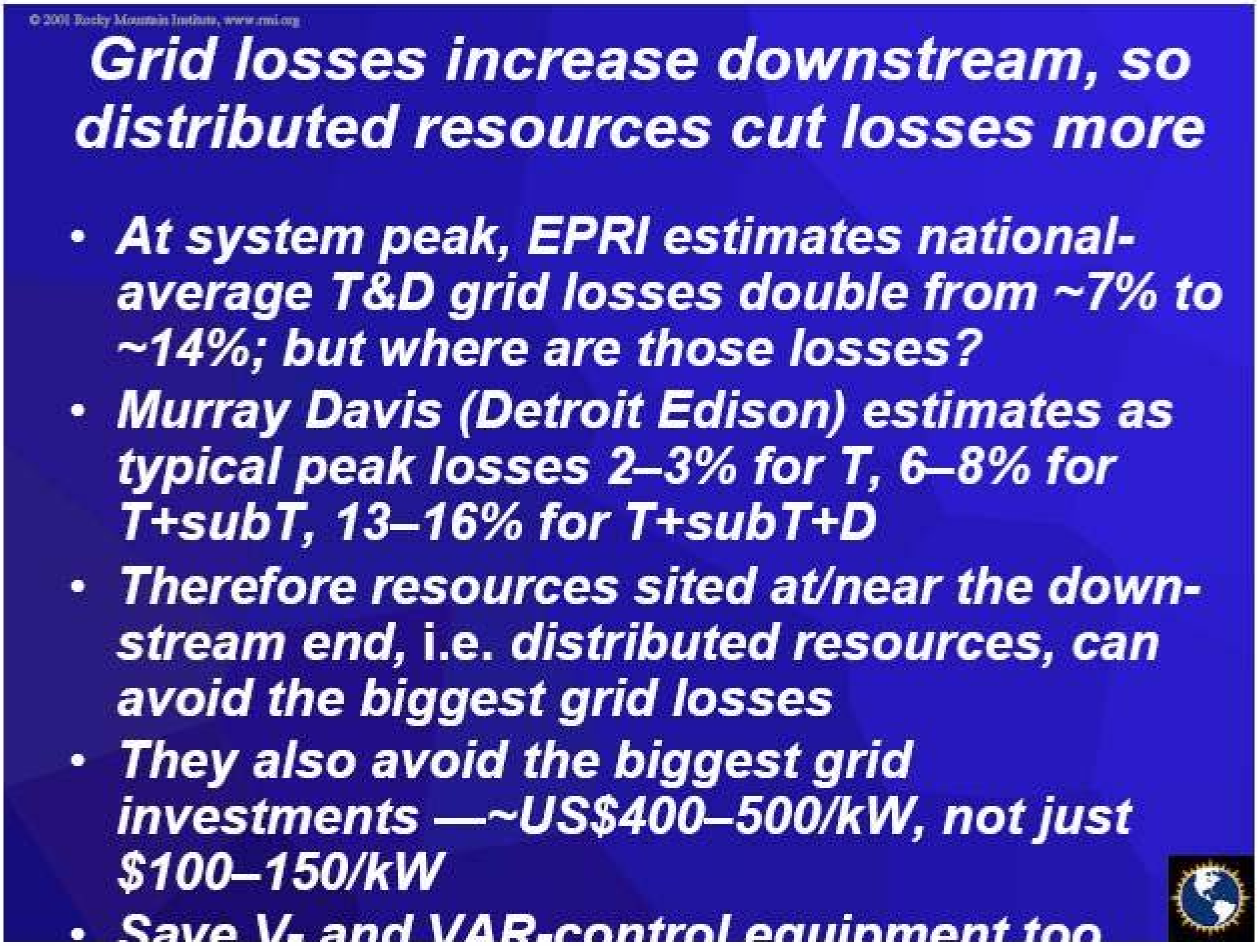
>>> "Bill Powers" <bpowers@powersengineering.com> 1/30/2008 10:57 AM >>>
Hello Don,

Quick question. I just came across this Rocky Mountain Institute slide from an Amory Lovins presentation a few years back. The CEC uses a 7.5% average transmission loss assumption for out-of-state transmission imports for GHG calculation purposes. That is consistent with the slide for average losses. However, the statement is made that EPRI estimates peak losses at 14% and a breakdown is provided for the distribution of these losses through the T&D system.

Does the CEC have a similar report that documents losses on average and at peak in the T&D system?

Thanks,

Bill Powers
Powers Engineering
619-295-2072



Grid losses increase downstream, so distributed resources cut losses more

- ***At system peak, EPRI estimates national-average T&D grid losses double from ~7% to ~14%; but where are those losses?***
- ***Murray Davis (Detroit Edison) estimates as typical peak losses 2–3% for T, 6–8% for T+subT, 13–16% for T+subT+D***
- ***Therefore resources sited at/near the downstream end, i.e. distributed resources, can avoid the biggest grid losses***
- ***They also avoid the biggest grid investments —~US$400–500/kW, not just $100–150/kW***
- ***Save V- and VAR-control equipment too***

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BEFORE THE
PUBLIC UTILITIES COMMISSION
OF THE
STATE OF CALIFORNIA

Order Instituting Rulemaking to Develop)
Additional Methods to Implement the California) Rulemaking: 06-02-012
Renewables Portfolio Standard Program) (Filed February 16, 2006)
)

Pre-Workshop Comments
of GreenVolts, Cleantech America, and Community Environmental Council
on the 2008 Market Price Referent

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6 March 2008

Locational Benefits of WDG

BEFORE THE
PUBLIC UTILITIES COMMISSION
OF THE
STATE OF CALIFORNIA

Order Instituting Rulemaking to Develop	)	
Additional Methods to Implement the California	)	Rulemaking: 06-02-012
Renewables Portfolio Standard Program	)	(Filed February 16, 2006)
	)	

Pre-Workshop Comments of GreenVolts, Cleantech America, and Community Environmental Council on the 2008 Market Price Referent

Pursuant to Administrative Law Judge Anne Simon's Ruling dated February 8, 2008 (ALJ Ruling), GreenVolts, Cleantech America, and Community Environmental Council (collectively the "Joint Parties") present opening comments on issues associated with the 2008 market price referent (2008 MPR). The Joint Parties' comments focus on Section 4.1.4 of the ALJ Ruling, which asks parties to discuss how locational pricing should be incorporated into the 2008 MPR. The Joint Parties' primary interest in this proceeding is ensuring that the locational benefits of intelligently-sited renewable energy generation are reflected fully in the 2008 MPR. Although locational pricing is the focus of these comments, the Joint Parties also have a strong interest in the other issues outlined in the ALJ Ruling, and support the comments on those matters that are being filed concurrently by the California Wind Energy Association (CalWEA), the California Cogeneration Council (CCC), and the Concentrated Solar Power companies (CSP).

GreenVolts is a San Francisco company with the mission of making solar energy economical. The company has developed state-of-the-art concentrating photovoltaic (CPV) technology that achieves unparalleled solar-to-electricity conversion efficiency through an innovative integration of optics and solar tracking. Like central station power plants, GreenVolts' technology is a complete power plant designed for delivering the lowest levelized cost of energy. Also, like traditional solar panels on roof-tops, GreenVolts' power plants are sited close to loads, increasing efficiency and further reducing cost. GreenVolts is currently constructing a California Public Utilities Commission (CPUC) approved (Resolution E-4132) solar power plant that will fulfill a 20-year power purchase agreement (PPA) with Pacific Gas & Electric (PG&E). This 2 MW power plant will be interconnected to PG&E's 12kV distribution lines near Tracy, California. In addition to having a high Generator Meter Multiplier (GMM), reflecting that generation at this delivery point already reduces system average line losses, the site is within two miles of a major new housing development that will become one of the largest loads in the region. GreenVolts expects to widely replicate such utility-scale wholesale distributed generation (WDG) solar power plants, which will deliver to California's ratepayers not only significant amounts of clean solar energy, but also the tangible and quantifiable locational benefits that are the subject of these comments.

Cleantech America, Inc. is a leading California-based developer of in-grid, emission-free, photovoltaic (PV) solar farms and other renewable energy projects sized 5 MW and greater. The company recently received approval from the CPUC for a 5 MW solar PV PPA with PG&E, the largest such contract with an IOU approved to date under the state's RPS program. Cleantech's business plan is, in part, to site projects near utility distribution or transmission systems close to serviced load. The company's in-grid strategy is intended to provide ratepayers with significant locational benefits, including improved air quality, avoided congestion costs, reduced need for major new bulk transmission, and regional green collar jobs growth. Coupled with the company's strategy to reduce the cost of PV and other solar electricity generation through economies of scale, locational pricing offers ratepayer benefits that are not currently reflected in the MPR.

The Community Environmental Council is a member-supported environmental non-profit organization formed in Santa Barbara in 1970 and is the leading environmental organization in the mid-California area. In 2004, the organization shifted its primary focus to energy and transportation issues and began spearheading a regional effort to wean communities from fossil fuels over the next two decades. The California Environmental Council combines community efforts on a number of energy and climate change-related issues with action on associated state and federal policy issues. The state and federal policy action is directly informed by the organization's extensive experience at the local level.

I. SUMMARY

The Joint Parties believe there is an underserved renewable energy market segment where renewable generation supplying wholesale power can be sited on utility distribution systems near significant loads. The renewable, wholesale distributed generation (WDG)[1] supplied by new technology like GreenVolts' promises to provide ratepayers with significant locational benefits, compared to large renewable projects that typically must be sited in remote locations where large tracts of land are available. The locational benefits of WDG include:

- avoiding the need for major new bulk transmission facilities,
- meeting local resource adequacy needs,
- reducing transmission line losses,
- avoiding congestion costs,
- reducing distribution line losses,
- avoiding demand-related distribution investments.

These benefits are not currently reflected in the MPR, which serves as the key pricing benchmark for new renewable generation. The MPR has been designed, like the entire RPS program, with a focus on large renewable projects that supply tens or hundreds of megawatts of wholesale power delivered into the bulk transmission system. However, state policy is beginning to recognize the potential of renewable WDG, through initiatives such as the AB 1969 "feed-in" tariffs whose price is set at the prevailing MPR. If California is to realize the full

---

[1] "Wholesale distributed generation" (WDG) projects are significantly distinguished from traditional "distributed generation" (DG), which generally refers to small, retail generation projects sized to serve a specific on-site load, with power flowing onto the utility distribution system only to the limited extent that on-site generation happens to exceed on-site load.

potential of renewable WDG, the MPR applicable to small renewable projects sited on the distribution system should reflect the enhanced benefits that ratepayers derive from the favorable location of this new renewable generation.

These comments respond to the ALJ’s Ruling asking whether the 2008 MPR should incorporate locational pricing, and explain how the 2008 MPR should be modified to include the locational benefits of WDG projects. The Locational Marginal Pricing (LMP) under the CAISO’s new Market Re-design and Technology Update (MRTU) program will provide data on transmission line loss and congestion benefits at thousands of locations on the CAISO grid. WDG projects can avoid the distribution line losses specified in the utilities’ Wholesale Distribution Access Tariffs (WDATs).

Finally, the Commission’s adopted E3 model for the avoided costs associated with energy efficiency programs includes a time-dependent, hourly valuation of avoided investment-related Transmission & Distribution (T&D) costs. This model can be used to value the avoided T&D costs from a WDG project; these costs should be added to the MPR applicable to the project. The Joint Parties are aware that the utilities have been reluctant to recognize that generators avoid T&D costs unless located in an area where specific costs can be avoided. In pursuit of benefits for all parties including ratepayers, the Joint Parties stand ready to work cooperatively with the utilities to identify those areas of their systems where the T&D benefits of WDG are at least as large as those specified in the E3 model, and to site renewable WDG projects in those areas. To encourage the development of renewable WDG generation, the Joint Parties recommend that the Commission direct the utilities to publish, by 31 December 2008, a list of the distribution substations on their systems where WDG would avoid T&D costs at least as high as those specified in the E3 model – in essence, a distribution-level version of the Transmission Ranking Cost Report that the utilities publish to indicate the availability and cost of bulk transmission on their systems.

II. JOINT PARTIES' INTEREST IN THIS PROCEEDING

The Joint Parties have studied the tangible and quantifiable locational benefits of wholesale distributed generation (WDG) – the market segment where utility-scale, wholesale energy is generated on the distribution network close to loads. The ability to locate renewable generation, and solar power plants in particular since those satisfy peak demand with ultra-clean energy, on the distribution network close to loads promotes local resource adequacy and avoids the challenges associated with expanding the state's transmission infrastructure. These challenges include costly transmission investment requirements; notoriously long planning, permitting and build-out times; the significant environmental impacts of new transmission lines; congestion bottlenecks; and the substantial line losses associated with the long-distance transmission of electricity. WDG also can reduce losses on the distribution system, avoid investments to expand the distribution system, and improve reliability by generating power close to where it is consumed.

Given that the MPR is the statutory benchmark for a reasonable, long-term market price for electricity from new renewable generation,[3] the MPR should recognize the enhanced benefits to ratepayers from the intelligent siting of new renewable generation at locations that offer the greatest benefit to ratepayers. Hence, the locational benefits of WDG should be incorporated into the MPR.

III. STATE POLICY IS JUST BEGINNING TO ADDRESS RENEWABLE WHOLESALE DISTRIBUTED GENERATION.

Despite the advantages of renewable WDG, this is a market that, until very recently, has been largely ignored by California's otherwise laudable efforts to promote development of renewable technologies for electric generation. For example, the incentives available under the California Solar Initiative (CSI) are limited to distributed generation (DG) facilities serving

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[2] P.U. Code Section 399.15(c).

retail, on-site loads and to projects producing no more than 1 MW. The RPS program is structured to award power purchase contracts to very large renewable generation projects delivering wholesale power into the state's transmission grid. Large RPS projects require significant land area in regions with abundant renewable resources, the combination of which are available predominantly in locations remote from the state's load centers. As a result, the availability of adequate bulk transmission is a major challenge for large RPS projects. Further, the successful participation in the full RPS solicitation process is a complex and expensive endeavor, which presents a significant barrier to small renewable WDG projects. GreenVolts and Cleantech America both have direct experience with the full cycle of the RPS request for offer (RFO) process, and both have found that the high cost and effort associated with participating in the solicitation process significantly diminishes the economic attractiveness of the RPS for small projects, certainly including projects with a capacity of 5 MW or less.

California is beginning to take initial steps to address the needs of renewable WDG. On February 14, 2008, the Commission issued Resolution E-4137, which gave final approval to what the Commission described as "feed-in" tariffs under which small renewable generators (with up to 1.5 MW in capacity delivered to the utility) can sell wholesale power to the state's investor-owned utilities under simplified 10-, 15-, or 20-year contracts. The price under these tariffs will be the prevailing MPR price. These feed-in tariffs were mandated in AB 1969, which the Commission subsequently implemented in Decision No. 07-07-027 and Resolution E-4137.[3]

The AB 1969 tariffs will be available for up to 480 MW of new renewable generation. 250 MW of this capacity will be available only to projects owned and operated by public water and wastewater agencies, but pursuant to D. 07-07-027 PG&E and Edison will make 230 MW of capacity available to small renewable projects at any site, with a size limit per project of up to 1.5 MW delivered to the utility.[4] The Commission noted that "these 'feed-in tariffs' present a

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[3] AB 1969 added P.U. Code Section 399.20.

[4] A project selling power to a utility under these tariffs can be larger than 1.5 MW, so long as the project serves an on-site load such that the utility purchases no more than 1.5 MW of the project's excess generation.

simple mechanism for small renewable generators to sell power to a utility at predefined terms and conditions, without contract negotiations." CPUC President Michael Peevey observed that the AB 1969 feed-in tariffs would allow small generators to participate in the RPS program, because "up until now, only large renewable generators were able to effectively participate in the RPS program."[5] The availability of AB 1969 contracts at the prevailing MPR price increases the importance of ensuring that the locational benefits of WDG are incorporated accurately into the 2008 MPR. As explained in more detail below, such WDG projects provide ratepayers with significant and quantifiable benefits associated with intelligent siting close to loads, and the value of these significant locational benefits is not yet reflected in the MPR price.

IV. LOCATIONAL VALUATION UNDER MRTU

Section 4.1.4 of the ALJ Ruling requests comments on how locational pricing should be incorporated into the 2008 MPR, particularly once locational marginal pricing is implemented under the CAISO's MRTU program. GreenVolts appreciates the Commission's recognition of the importance of locational pricing; it is of particular importance to WDG, such as the WDG solar power plants that GreenVolts is developing.

Renewable WDG is generally interconnected to a utility's distribution system and produces more power than is needed by any on-site load. The excess power exported to the grid typically is consumed by nearby loads served from the same distribution system to which the generator is connected. The locational value of such generation is not captured in the current MPR, which is designed as a benchmark for large, transmission-level RPS projects comparable in size to the 500 MW combined-cycle gas turbine (CCGT) facility on which the MPR is based. The MPR is a statewide value designed to capture a "representative statewide" estimate for the

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[5] See the CPUC's February 14, 2008 press release, "CPUC Approves Feed-In Tariffs...," available at http://docs.cpuc.ca.gov/WORD_PDF/NEWS_RELEASE/78824.PDF.

costs of a new CCGT plant built in California.[6] The MPR calculation uses a 50/50 average of the delivered costs of natural gas in northern and southern California, and includes a line loss adjustment based on an average of line losses only on the California Independent System Operator's (CAISO) transmission grid. Thus, the current MPR represents the statewide average cost of large amounts of wholesale electricity delivered to the load center at transmission voltages.

Renewable WDG such as GreenVolts' Tracy project will provide locational benefits to California ratepayers that are not now reflected in the MPR, including:

- lower transmisison line losses,
- lower intra-zonal congestion,
- reduced distribution line losses, and
- avoided transmission and distribution investments.

Each of these benefits is discussed in the sections below. MRTU will enable the more accurate pricing of the first two of these benefits, and the Commission has existing methodologies to value the other two, which are discussed in Section V.

A. Transmission Line Losses.

Today, GMMs are used for the locational valuation of line loss impacts on the CAISO transmission grid. GMMs measure the average transmission line losses to deliver power to a virtual load center. The MPR price is adjusted by the system average GMM,[7] and the Joint Parties understand that typical RPS contracts pay renewable generators for their generation adjusted by their site-specific GMM.

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[6] See D. 03-06-071, at 21.

[7] Currently, the system average GMM used in the MPR model is the simple average of the GMMs on the CAISO grid. The use of the simple average GMM appears to understate average transmission losses on the CAISO grid; the accurate representation of CAISO system line losses would be the average GMM weighted by the output of each generator. The Joint

The valuation of line losses will change under MRTU. The new LMP method will provide a line loss component of the market price at each node. This market-based loss component will reflect marginal losses at each node, a significant change from the GMM methodology, which uses losses scaled to system average losses. Under MRTU, the CAISO also will provide aggregated losses across all of the nodes on its system and across each utility's service territory. For example, assume a new renewable generator's node has an annual average loss component of $1.50 per MWh vs an annual system average loss component of $2.00 per MWh. The MPR applicable to that project should be increased by $0.50 per MWh to reflect the ratepayer benefit of the reduced losses associated with that project's favorable location. In this way, an MPR specific to each project could be determined, in order to reflect accurately a project's site-specific annual losses under MRTU compared to the system average losses.

B. Congestion

Today, intra-zonal congestion is not priced in the market or in the MPR. However, under MRTU, the explicit valuation of intra-zonal congestion at each node will be possible, as congestion, like line losses, also will be an explicit component of the LMP price at each node. It will be possible to calculate system average congestion costs and to include them in the statewide MPR. Most important, similar to line losses, the MPR applicable to a specific project could be adjusted to reflect a project's site-specific annual congestion costs under MRTU, compared to the system's annual average congestion costs measured either over the whole CAISO system or over the purchasing utility's service territory.

C. MRTU Timing

While MRTU is not expected to "go live" until the September 2008 time-frame, the Commission should work toward incorporating MRTU line loss and congestion constructs into the 2008 MPR. The Joint Parties urge the Commission to devote effort at the upcoming workshop to incorporate MRTU constructs into the 2008 MPR. Active participation by CAISO and Energy Division personnel familiar with LMP pricing should make this process effective.

Parties support the comments of CalWEA / CCC / CSP on this point.

V. AVOIDED TRANSMISSION AND DISTRIBUTION COSTS

Renewable WDG located on the distribution system, and serving local loads, can allow the IOUs to avoid both distribution losses and investment-related T&D costs. The impact of WDG will be to reduce demand on the distribution system, just as on-site DG and energy efficiency/demand-side management programs effectively reduce distribution system loads. As discussed below, the Commission has well-established tools to evaluate the benefits of such reductions.

A. Avoided Distribution Losses

The Commission has long recognized that QF generation located on the distribution system allows the utilities to avoid distribution system losses.[8] The Commission generally has looked to the utilities' Wholesale Distribution Access Tariffs (WDAT) as the source for avoided distribution losses. For example, in the Commission's most recent review of QF line losses – D. 01-01-007 – the Commission adopted Southern California Edison's and San Diego Gas & Electric's WDAT distribution loss factors as the measure of the distribution line losses avoided by QFs that deliver into the distribution systems of these utilities.[9] **Table 1** below summarizes the existing WDAT loss factors of the three major California IOUs, and recommends that they be used to assess the benefits of WDG in avoiding line losses on the distribution system. As losses increase significantly during periods of high demand, the Joint Parties submit that the use of these average loss factors will be conservative for renewable peaking projects. The MPR applicable to renewable WDG interconnected to the distribution system should be increased by one plus the distribution loss factors in Table 1, as given by the following formula:

WDG Distribution Loss Factor = 1 / (1 – WDAT Energy Loss Factor)

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[8] D. 82-12-120, D.84-03-092, and D.87-12-066.

[9] D. 01-01-007, at 18 and Conclusion of Law 15.

Table 1: *Utility WDAT Energy Loss Factors*

Utility	Distribution Voltage	WDAT Energy Loss Factors
PG&E	Primary	1.25%
	Secondary	3.62%
SCE	Subtransmission	1.12%
	Primary	3.73%
SDG&E	All voltages	0%

Sources: PG&E WDAT tariff, D. 01-01-007 (SCE and SDG&E).

B. Avoided T&D Investments

The question of whether generation interconnected at the distribution-level, or energy efficiency programs that reduce end-use demand, allow the utilities to avoid T&D investments has been the subject of considerable debate. The Commission's adopted E3 model for the avoided costs associated with energy efficiency programs includes a time-dependent, hourly valuation of avoided investment-related T&D costs. The E3 model uses system-wide measures of avoided T&D costs – typically, marginal T&D costs calculated for use in electric rate design. When the Commission reviewed the E3 model in 2004 - 2005, the utilities opposed the inclusion of avoided T&D costs in the model, arguing that energy efficiency resources avoid T&D costs only in certain specific, case-by-case circumstances, such as on a rapidly-growing distribution circuit where an upgrade is needed in the near future.[10] The Commission rejected this position in D. 05-04-024, finding that "while a case-by-case analysis should be applied to determine payments related to specific projects for long-term conservation measures it is appropriate to credit programs with T&D avoided costs for program evaluation purposes."[11] The Joint Parties submit that the primary purpose of the MPR is to provide a benchmark for the RPS contract costs that ratepayers should bear; in effect, to determine what level of RPS program costs are fair and cost-effective for ratepayers to support. This function is similar to the use of the E3 model to

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[10] *See* D. 05-04-024, at 35-36.

develop cost-effectiveness tests "for program evaluation purposes." From this perspective, it would be appropriate for the MPR to recognize generally that distribution-level generators can avoid investment-related T&D costs.

Additionally, the MPR is beginning to be used as a price for direct payments to certain renewable generators – for example, the MPR price is used directly in the AB 1969 feed-in tariffs. The Joint Parties expect that the utilities will oppose the use of the E3 model's avoided T&D costs as a component of the MPR used for such payments, unless the avoidance of such costs can be specifically documented "in the field." Hence, the Joint Parties propose to work cooperatively with the IOUs' T&D planners to identify sites that offer greater T&D benefits than the average avoided T&D values produced by the E3 model. GreenVolts and Cleantech welcome the opportunity to cooperate with the utilities to locate solar WDG at sites on the utility distribution systems where the solar peaking generation provides the greatest benefits for ratepayers, in terms of meeting load growth and peak period demands, and thus avoiding T&D investments. Projects sited in this cooperative way should receive an adder to their MPR value equal to the expected avoided T&D costs calculated by the adopted E3 model. The avoided T&D costs in the E3 model are average values for each IOU division or planning region. As a result, if renewable WDG is sited in locations with higher-than-average incremental T&D costs, ratepayers would be assured that they have received excess value if the MPR for such projects only includes average avoided T&D costs for that area, as calculated by the E3 model.

The E3 model's time-dependent valuation of avoided T&D costs includes avoided T&D costs for each hour of the year, and for each IOU division or planning region. Given the hourly output profile of a new renewable generator, the model can easily calculate an "avoided T&D adder" for that generator that could be added to the MPR applicable to the project. The general formula for such a WDG T&D adder is as follows:

$$\textit{\textbf{WDG T\&D Adder}} = \Sigma_{\textit{All hours}}\ \textit{\textbf{[E3 T\&D Costs x WDG Generation]}} / \Sigma_{\textit{All hours}}\ \textit{\textbf{WDG Generation}}$$

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[11] *Ibid.,*at 36.

Table 2 shows the results from using the E3 model to calculate such avoided T&D adders for each IOU division or planning region included in the E3 model, for both a baseload (7x24) output profile and for a representative solar photovoltaic (PV) output profile from a south-facing flat-plate PV system at a 38.5 degree tilt located in Sacramento, California. Table 2 also shows T&D breakouts. Note that the E3 model calculates that the solar generation profile produces about 75% of the avoided T&D benefits of the baseload profile; this is because PV output is high during the peak afternoon hours when peaks occur on the distribution system.

The Joint Parties note that actual experience with behind-the-meter solar DG developed under the Commission's Self Generation Incentive Program (SGIP) is beginning to validate the ability of distributed PV systems to reduce peak demands on utility distribution systems. The August 2007 evaluation report on the SGIP program shows that, in the summer of 2006, installed PV systems reduced distribution line loadings on peak summer afternoons by 42% to 56% of the PV systems' installed capacity.[12] The evaluation consultant, Itron, concluded that "SGIP technologies are seen to provide the potential for significant reduction in peak loading of the distribution system."[13] Itron noted a number of reasons why SGIP projects have not achieved an even greater level of capital-related savings on the distribution system:

> In addition to limited penetration of SGIP facilities within the distribution system, a number of other factors contribute to a lack of distribution capital savings. One of these is that the SGIP generators operate independently of the distribution system. Therefore, the SGIP owner does not know when the distribution peak is, nor do they have any incentive to operate during the peak even if they did know. In fact, the current SGIP rules prohibit an additional incentive to operate during the local capacity peak. Similarly, the distribution utility planners do not necessarily know which SGIP generators are being served by overloaded equipment, likely because the penetration of SGIP generators is not currently high enough to warrant close attention for capacity planning at the distribution level. In addition, SGIP owners choose where to install their systems, not the utility; therefore, there are not a concentrated number of installations in a single area of need that could provide significant load relief on a particular overloaded feeder or substation.[14]

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[12] GreenVolts' PV technology tracks the sun, and thus will sustain its output at higher levels than flat-plate PV over the course of a peak summer afternoon. As a result, GreenVolts' plants will achieve higher reductions in distribution line loadings, as a percent of project capacity, than the flat plate PV systems installed under SGIP.

[13] Itron, "CPUC Self-Generation Incentive Program – Sixth Year Impact Evaluation Report" (August 30, 2007), at Table 4-1 and pages 1-10 to 1-14.

[14] *Ibid.*, at 5-28.

E3 Model T&D Values (Levelized 20-year in 2008$)

		Transmission + Distribution				Transmission				Distribution			
Utility	Division	Baseload Profile		Solar Profile		Baseload Profile		Solar Profile		Baseload Profile		Solar Profile	
		$/kW-year	$/MWh	$/kW-year	$/MWh	$/kW-year	$/MWh	$/kW-year	$/MWh	$/kW-year	$/MWh	$/kW-year	$/MWh
PG&E	Central Coast	$46.07	$5.26	$35.70	$24.60	$1.55	$0.18	$1.20	$0.83	$44.51	$5.08	$34.50	$23.77
	De Anza	$58.67	$6.70	$46.95	$32.35	$1.55	$0.18	$1.24	$0.86	$57.11	$6.52	$45.71	$31.49
	Diablo	$55.62	$6.35	$44.51	$30.67	$1.55	$0.18	$1.24	$0.86	$54.06	$6.17	$43.27	$29.81
	East Bay	$11.57	$1.32	$8.97	$6.18	$1.55	$0.18	$1.20	$0.83	$10.02	$1.14	$7.77	$5.35
	Fresno	$48.24	$5.51	$37.08	$25.55	$1.55	$0.18	$1.19	$0.82	$46.68	$5.33	$35.89	$24.72
	Kern	$30.87	$3.52	$23.73	$16.35	$1.55	$0.18	$1.19	$0.82	$29.32	$3.35	$22.54	$15.53
	Los Padres	$46.82	$5.34	$37.47	$25.81	$1.55	$0.18	$1.24	$0.86	$45.26	$5.17	$36.23	$24.96
	Mission	$70.36	$8.03	$54.53	$37.57	$1.55	$0.18	$1.20	$0.83	$68.80	$7.85	$53.32	$36.74
	North Bay	$47.46	$5.42	$36.78	$25.34	$1.55	$0.18	$1.21	$0.83	$45.90	$5.24	$35.57	$24.51
	North Coast	$64.43	$7.35	$40.41	$27.84	$1.55	$0.18	$0.97	$0.67	$62.87	$7.18	$39.43	$27.17
	North Valley	$80.30	$9.17	$63.33	$43.63	$1.55	$0.18	$1.23	$0.84	$78.74	$8.99	$62.10	$42.78
	Peninsula	$20.90	$2.39	$16.19	$11.16	$1.55	$0.18	$1.20	$0.83	$19.34	$2.21	$14.99	$10.33
	Sacramento	$60.93	$6.96	$48.05	$33.11	$1.55	$0.18	$1.23	$0.84	$59.37	$6.78	$46.83	$32.26
	San Francisco	$16.89	$1.93	$13.09	$9.02	$1.55	$0.18	$1.20	$0.83	$15.34	$1.75	$11.89	$8.19
	San Jose	$44.65	$5.10	$35.74	$24.62	$1.55	$0.18	$1.24	$0.86	$43.10	$4.92	$34.49	$23.76
	Sierra	$66.84	$7.63	$52.71	$36.32	$1.55	$0.18	$1.23	$0.84	$65.29	$7.45	$51.49	$35.47
	Stockton	$69.90	$7.98	$55.94	$38.54	$1.55	$0.18	$1.24	$0.86	$68.34	$7.80	$54.69	$37.68
	Yosemite	$42.73	$4.88	$34.20	$23.56	$1.55	$0.18	$1.24	$0.86	$41.18	$4.70	$32.96	$22.70
SCE	Dominguez Hills	$45.91	$5.24	$32.93	$22.69	$26.09	$2.98	$18.71	$12.89	$19.82	$2.26	$14.21	$9.79
	Foothills	$59.90	$6.84	$42.96	$29.59	$26.09	$2.98	$18.71	$12.89	$33.80	$3.86	$24.24	$16.70
	Santa Ana	$55.19	$6.30	$39.58	$27.27	$26.09	$2.98	$18.71	$12.89	$29.10	$3.32	$20.87	$14.38
	SCE Rural	$72.95	$8.33	$53.87	$37.11	$26.09	$2.98	$19.27	$13.27	$46.86	$5.35	$34.60	$23.84
	Ventura	$57.57	$6.57	$41.29	$28.45	$26.09	$2.98	$18.71	$12.89	$31.48	$3.59	$22.58	$15.56
SDG&E	SDG&E	$114.15	$13.03	$84.35	$58.11	$13.84	$1.58	$10.23	$7.05	$100.31	$11.45	$74.12	$51.07

Note: assumes 2008 - 2027 project lifespan, 2.5% inflation, 8.93% discount rate, and 2008 $

As set forth in these comments, the Joint Parties believe that WDG projects can address benefit constraints associated with capacity limitations of behind-the-meter PV systems under SGIP. Renewable WDG is thereby positioned to amplify the well documented tangible and quantifiable locational T&D benefits already being reaped by DG and SGIP projects. Of course, properly compensated renewable WDG will also assure that this important market segment develops effectively so it can help to deliver the achievement of RPS objectives on schedule.

The Joint Parties strongly believe the best way for the Commission to promote renewable WDG is to encourage the utilities and developers such as GreenVolts and Cleantech to work cooperatively to identify sites that offer the greatest benefits to ratepayers, in terms of avoiding T&D investments. The MPR applicable to such renewable WDG projects should include avoided T&D costs as determined by the Commission's adopted E3 model. In order to encourage the broadest development of WDG technologies, the utilities should make public to interested parties the locations on their systems where WDG would have benefits greater than the average avoided T&D costs contained in the E3 model. Accordingly, the Joint Parties recommend that Commission direct the utilities to publish, by 31 December 2008, a list of the distribution substations on their systems where WDG would allow the utility to avoid T&D costs at least as high as those specified in the E3 model. In essence, this list would constitute a distribution-level version of the Transmission Ranking Cost Report that the utilities publish to indicate the availability and cost of bulk transmission on their systems.

VI. CONCLUSION

Renewable WDG provides significant and quantifiable locational benefits to the RPS program and to the ratepayers of California; and renewable WDG should be compensated through MPR for its true and reasonable value. This proposal addresses an existing "gap" in the CPUC's programs that encourage renewable generation. Projects in the 1 to 5 MW range are currently underserved: They exceed the qualification limits for CSI or SGIP incentives plus net metering; and they are smaller than what was envisioned with the RPS program and the large overhead costs associated with participating in the standard RPS process. Renewable WDG such as GreenVolts' solar technology can be sited in load centers on distribution systems that serve significant local loads; thereby delivering substantial locational benefits. A feed-in tariff at the MPR price and with simplified standard contracts are now available to renewable WDG projects that are 1.5 MW or smaller, which will help to alleviate transaction costs for the smallest of the renewable WDG projects, but the large costs associated with participating in RPS solicitations, and negotiating contracts with the utilities, are challenging to leverage over a broader range of project sizes, definitely including projects up to 5 MW. As such, the AB 1969 feed-in tariff provides an important model.

The MPR, however, still needs to be modified to reflect the tangible and quantifiable locational benefits of renewable WDG. Proper reflection of these tangible and quantifiable benefits will stimulate development of this highly beneficial generation; thereby delivering the advantages of the currently underserved renewable WDG market segment to California, including higher probability of achieving RPS objectives <u>on schedule</u> and providing both environmental and <u>economic value</u> to California's ratepayers. Importantly, GreenVolts and Cleantech are ready to work cooperatively with utilities to locate solar WDG where the addition of renewable peaking generation will provide the greatest benefits to ratepayers.

Finally, the Joint Parties support the comments on other 2008 MPR issues filed by other parties representing renewable and distributed generators (e.g. CalWEA/CCC/CSP).

GreenVolts, Cleantech, and Community Environmental Council appreciate the Commission's attention to these comments, and look forward to participating actively in the upcoming 2008 MPR workshop.

Respectfully submitted,

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6 March 2008

CERTIFICATE OF SERVICE

I hereby certify that on this 6th day of March 2008, I have caused a copy of the foregoing

Pre-Workshop Comments
of GreenVolts, Cleantech America, and Community Environmental Council
on the 2008 Market Price Referent

to be served on all known parties to R0602012 listed on the most recently updated service list available on the California Public Utilities Commission website, via email to those listed with email addresses and via US mail to those without.

/s/ CRAIG LEWIS
Craig Lewis

Service List for R0602012

(last changed 4 March 2008)

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The Power and Potential of CdTe

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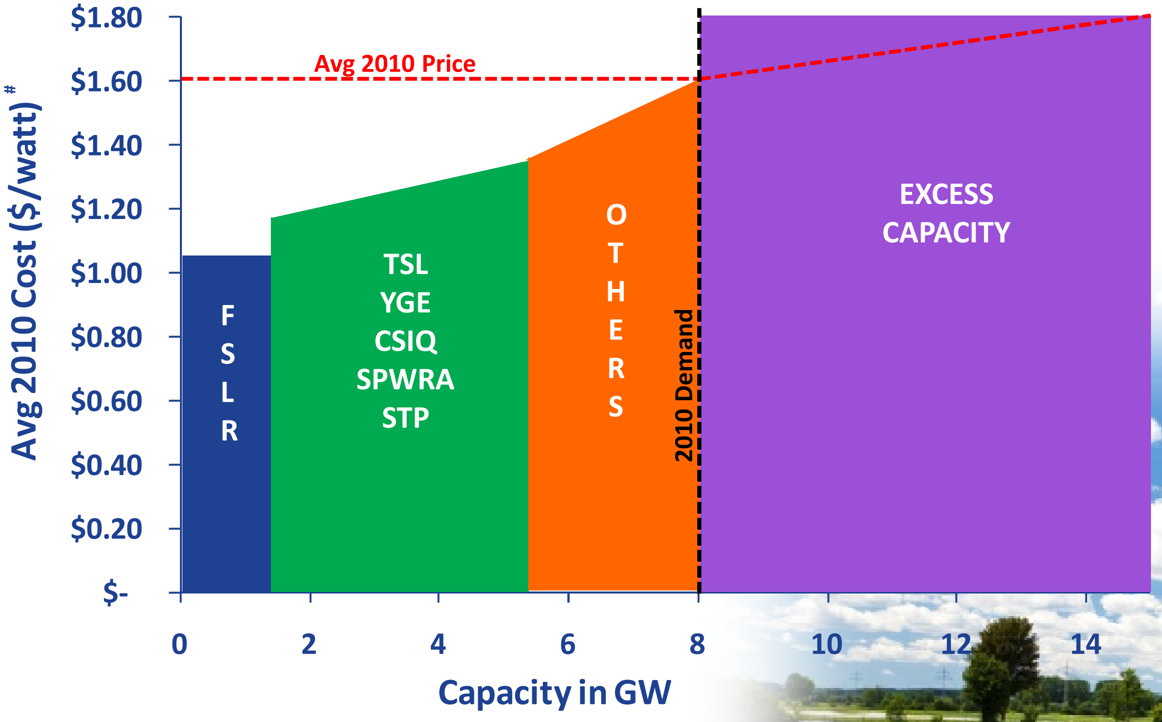
2010 PV Supply, Demand, and Opportunity

Capacity in GW vs. Average Cost for 2010*



#Cost adjusted for efficiency penalty or credit
*Source: Company data, Fulcrum estimates

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CdTe Competitive Landscape

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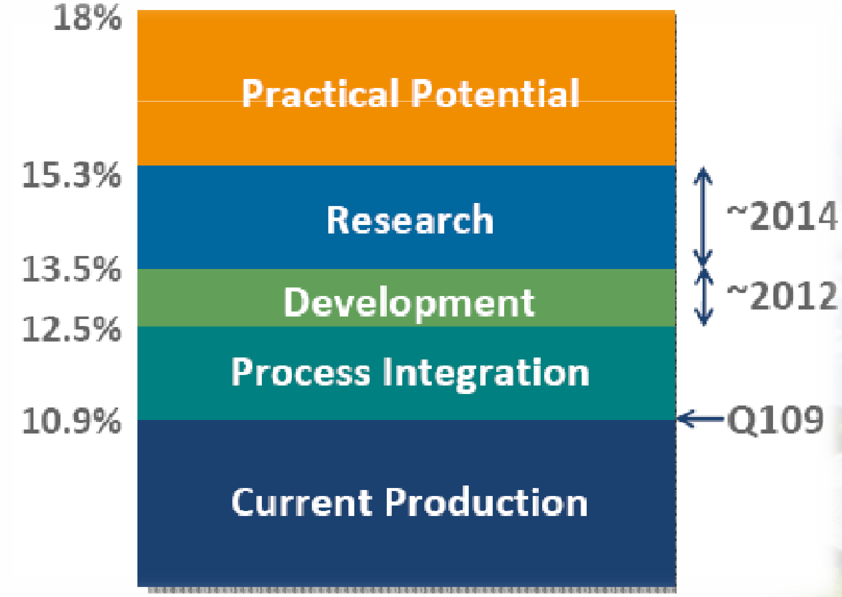
CdTe Potential

PrimeStar Solar

CdTe Technology	Lab Cell	Estimated Full Module
Present module technology		11%
NREL CdTe world record cell technology	16.5%	13%
CdTe potential with R&D improvements	19%	15%
Simulated near ideal CdTe technology	24%	19%

First Solar



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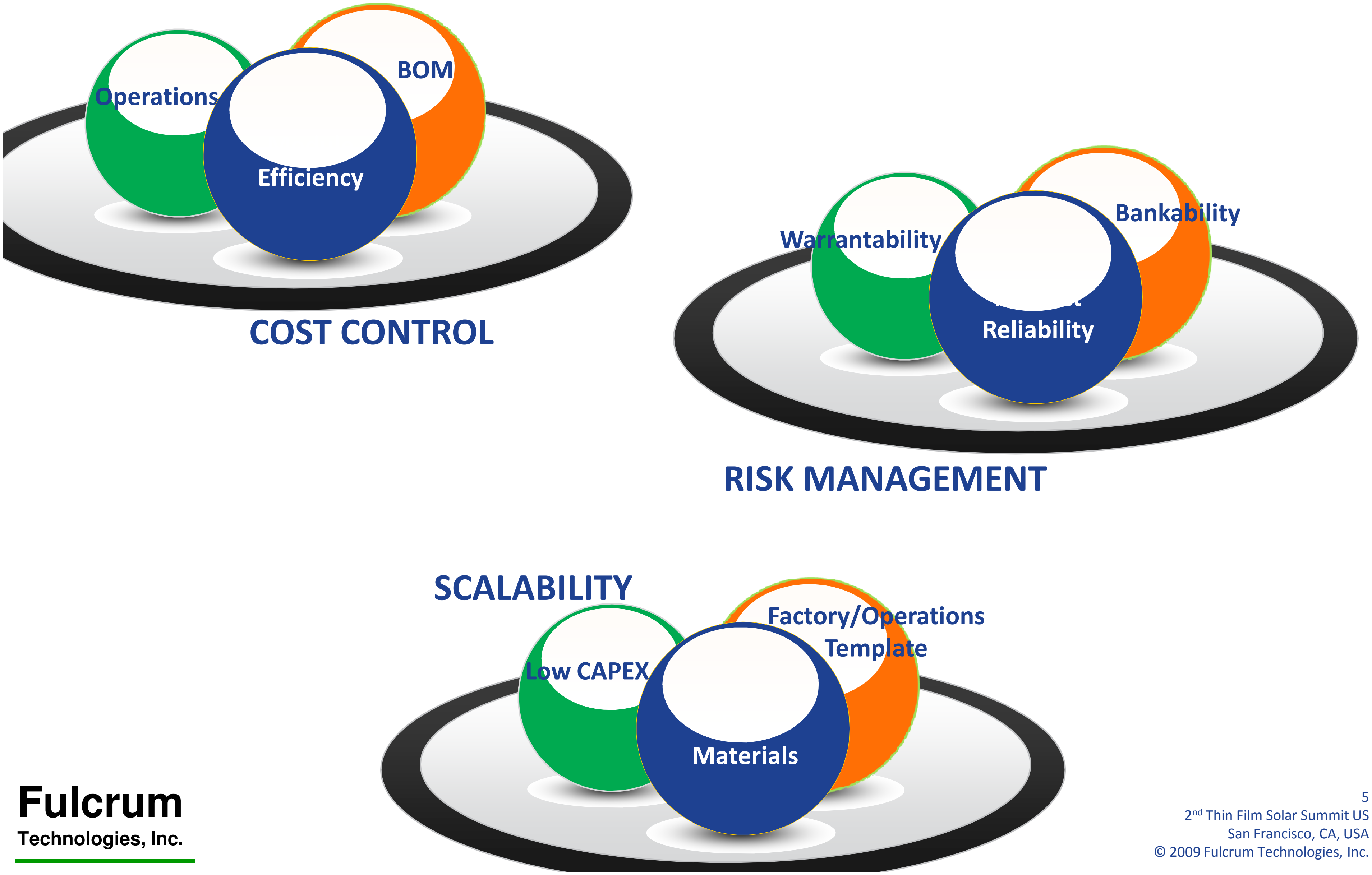
Recipe for Leadership



Operations

BOM

Efficiency

COST CONTROL

Warrantability

Bankability

Reliability

RISK MANAGEMENT

SCALABILITY

Low CAPEX

Factory/Operations Template

Materials

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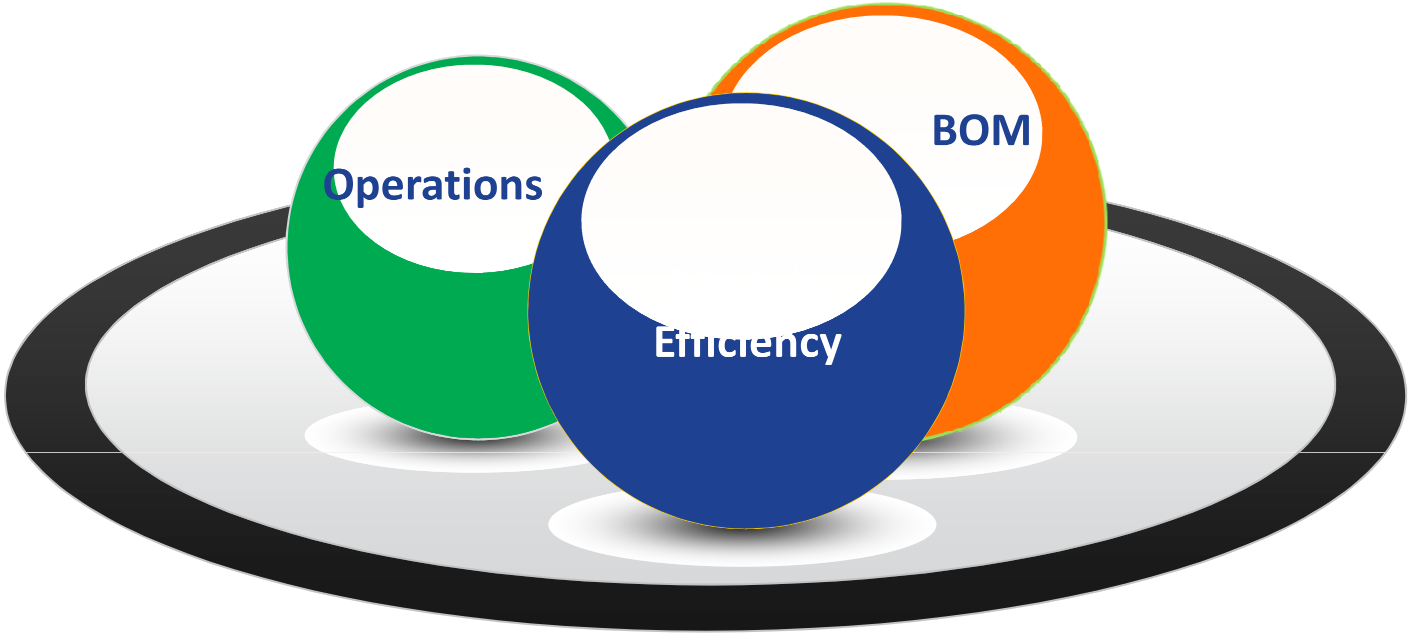
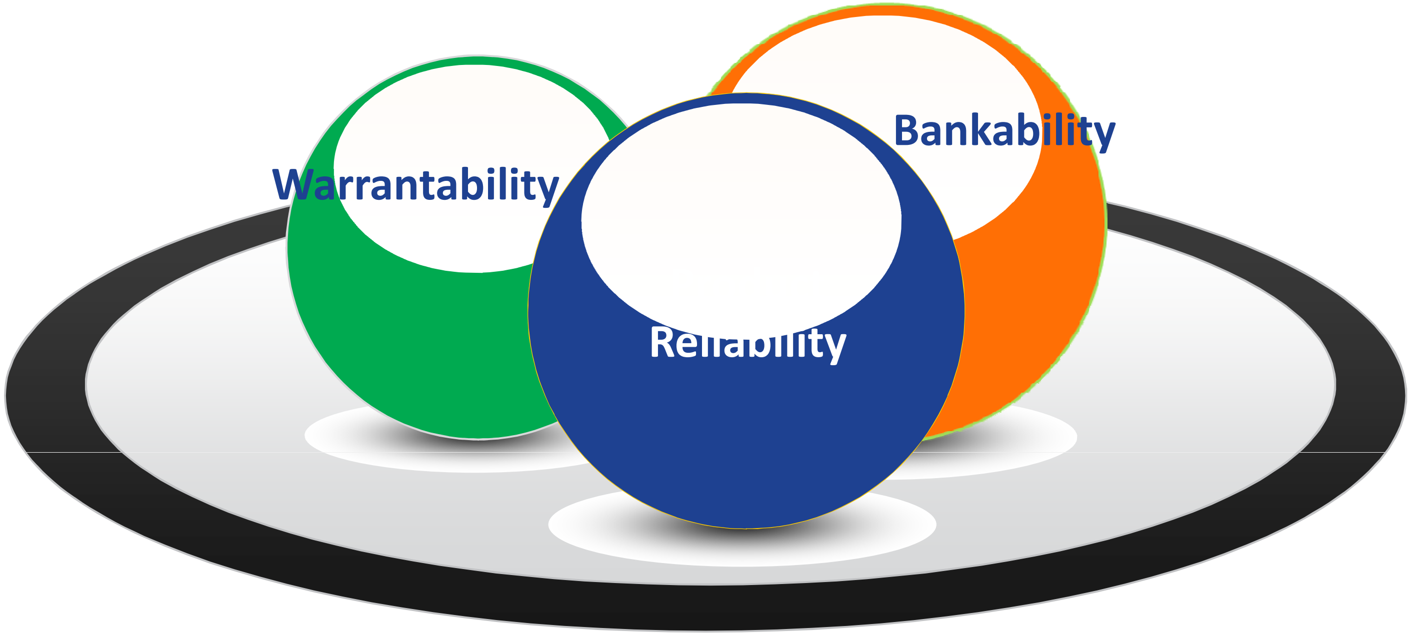
Cost Control



Cost = $0.85/watt

Risk Management



Installed Base = 1.5 GW

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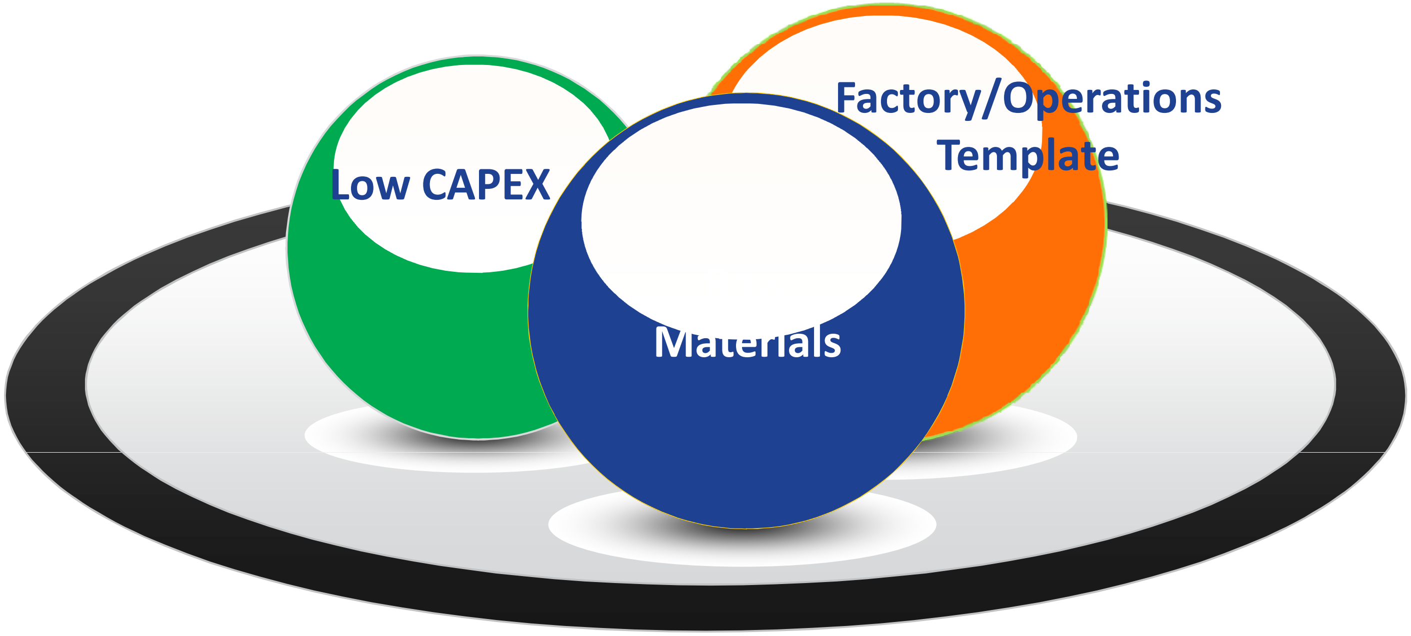
Scalability



CAPEX = \$0.60/watt

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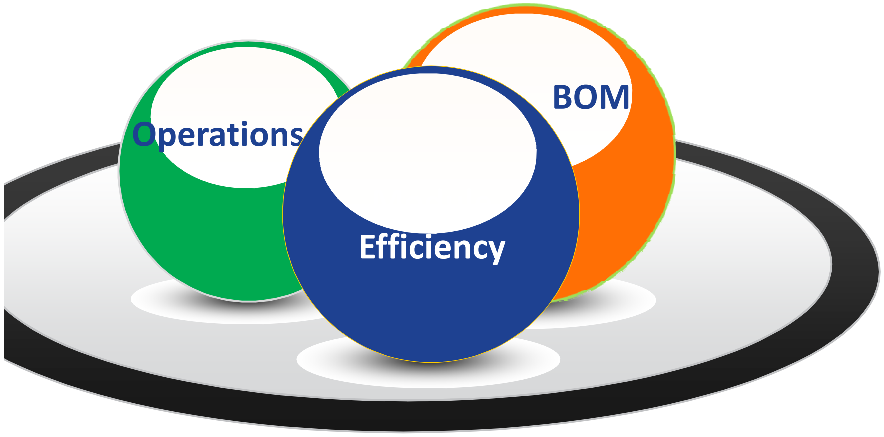
CdTe Leadership in PV



COST CONTROL

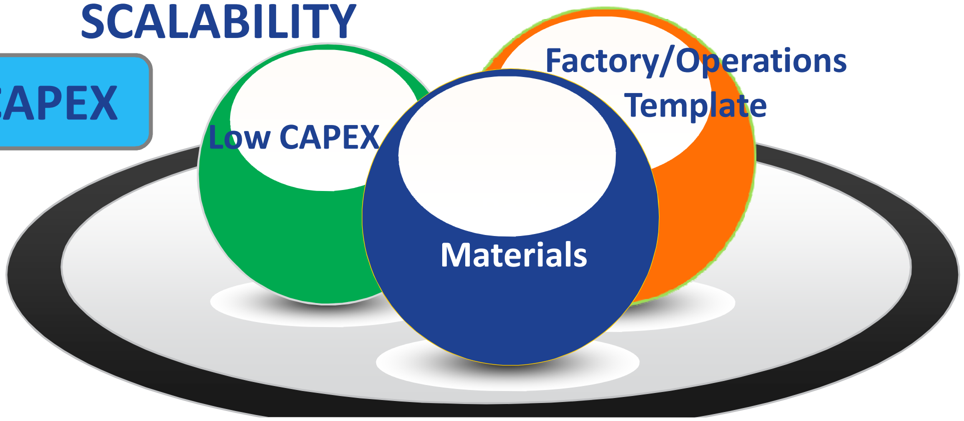
Cost = $0.85/watt

RISK MANAGEMENT

~1.5 GW installed

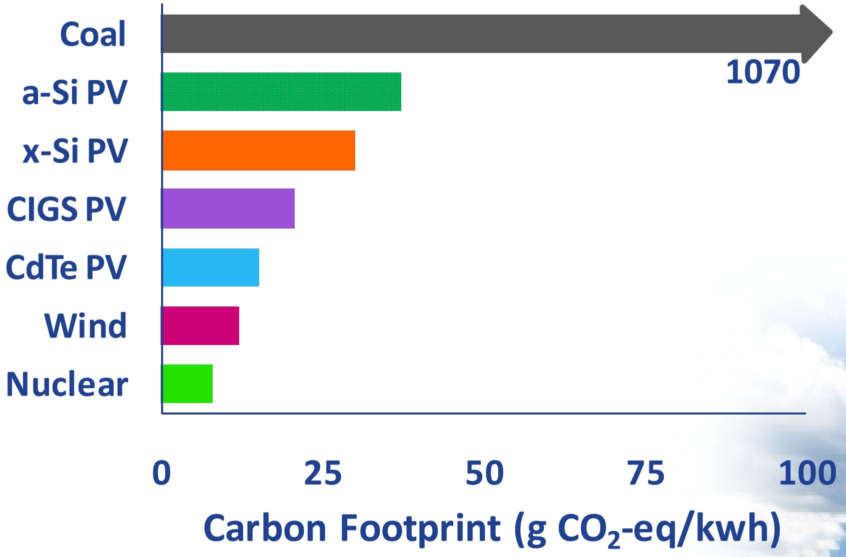
SCALABILITY

$0.60/watt CAPEX

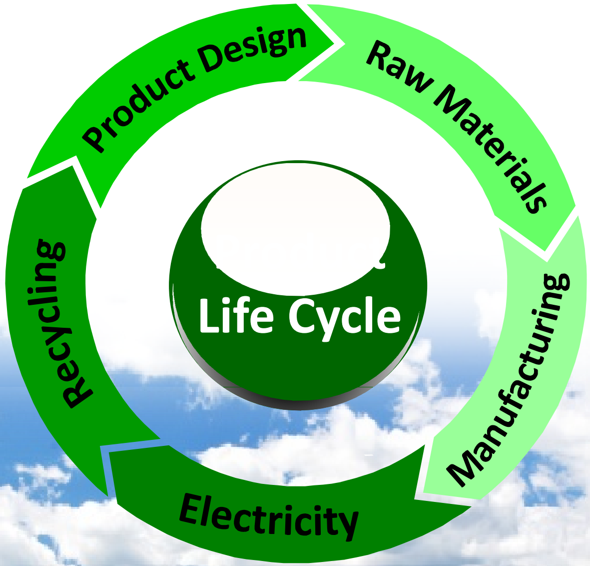


Environmental Awareness

Carbon Footprint of Electricity Generation Technologies*



[#] Adopted from ECN and M&W Zander presentation at Thin Film Industry Forum, Berlin, April 24, 2009



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Translocation of urban Gila Monsters: a problematic conservation tool

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Received 10 February 2003; received in revised form 24 June 2003; accepted 17 July 2003

Abstract

The Gila Monster (*Heloderma suspectum*) is a large, venomous lizard protected throughout its distribution in the southwestern United States and northwestern Mexico. Rapid urban growth in key areas of its range and increased encounters with humans prompted us to investigate translocation as a conservation tool with "nuisance" Gila Monsters. Twenty-five Gila Monsters reported as nuisances by residents in the northeastern Phoenix Metropolitan Area were translocated from 0 to 25,000 m from their point of capture. Subjects ($N = 18$) translocated less than 1000 m returned to their original site of capture within 2–30 days; none of those ($N = 7$) translocated more than 1000 m successfully returned, they exhibited high daily rates of speed, and were deprived the use of familiar refuges. We conclude that small distance translocations within suitable habitats are ineffective in removing Gila Monsters from areas deemed unsuitable. Moreover, individuals moved significantly greater distances are unlikely to remain at a translocation site, and may experience a variety of costs (e.g., predation risk) associated with high rates of movement.

Keywords: Gila Monster; Translocation; Sonoran Desert; Phoenix; Reptilia; *Heloderma suspectum*

1. Introduction

> "With the possible exception of the vampire bat, no other North American animal has been the source of more superstitions, the subject of as many legends, or the object of more exaggerated claims than the Gila Monster. Brown and Carmony (1991)"

Human populations are rapidly increasing in the American Southwest, and interactions with wildlife, especially top-order carnivores, are rising sharply. The likely outcome, especially for larger taxa, will be local extinctions due primarily to habitat loss and to a lesser extent, direct interactions with residents. One response to these threats is translocation (i.e., movement of wild individuals from one part of their range to another) of individuals to protected or intact habitat patches removed from areas of common interaction with humans. Fischer and Lindenmayer (2000) reviewed translocation studies of animals, and concluded that this technique fails to solve human-animal conflicts satisfactorily. Given the widespread use of translocation as a conservation method (see reviews in Fischer and Lindenmayer, 2000; Shine and Koenig, 2001; Nowak et al., 2002), it warrants further scrutiny, especially for unconventional, nongame animals such as reptiles.

Translocation efforts with some species are complicated due to their potential threat to humans, such as a venomous bite (Shine and Koenig, 2001; Nowak et al., 2002). One of the most notorious, large venomous reptiles encountered by residents in the southwestern United States is the Gila Monster (*Heloderma suspectum*), one of two species of helodermatid lizards and closely related to Old World varanids (Pregill et al., 1986; Schwenk, 1988; Bernstein, 1999). Gila Monsters are perhaps perceived as less threatening than other venomous reptiles such as rattlesnakes (*Crotalus* spp.), but they remain misunderstood by the public and experience many of the same conservation issues facing rattlesnakes as a result of urbanization. Translocation of venomous reptiles is widely practiced in metropolitan regions; each year many hundreds of rattlesnakes and

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doi:10.1016/j.biocon.2003.07.002

dozens of Gila Monsters are removed from residences and other locations in the Phoenix and Tucson metropolitan areas of Arizona, USA, and translocated to nearby desert habitats (Hare and McNally, 1997; Nowak et al., 2002; Mike Demlong, pers. comm.). Although recent reviews of results of translocation studies involving reptiles revealed consistently low success rates for snakes (Dodd and Seigel, 1991; Reinert and Rupert, 1999; Plummer and Mills, 2000; Nowak et al., 2002), Gila Monsters remain unstudied.

The secretive habits of Gila Monsters have contributed to a lack of knowledge on the part of biologists, as well as public misunderstanding. In spite of this, the Gila Monster was one of the first venomous reptiles to receive legal protection (Grant, 1952; Brown and Carmony, 1991; Bogert and Martin del Campo, 1993). In response to threats of commercial overcollecting for roadside menageries, zoological supply companies, and related venues, the Arizona Game and Fish Commission provided the initial steps in 1950 to legally protect Gila Monsters in Arizona. Subsequently, other states (Nevada—1969; Utah—1971; New Mexico—1975; California—1980), as well as Mexico, provided similar legal protection to Gila Monsters. Moreover, the Gila Monster is provided international protection under CITES (Convention on International Trade in Endangered Species).

The Gila Monster is chiefly a denizen of the Sonoran Desert, and it ranges from the southwestern United States to northwestern Mexico, primarily in Sonora (Campbell and Lamar, 1989; Brown and Carmony, 1991; Bogert and Martin del Campo, 1993). In the United States, it has large populations in Arizona, and peripheral populations in the Mojave, Great Basin, and Chihuahuan deserts (Campbell and Lamar, 1989; Bogert and Martin del Campo, 1993). Substantial populations likely occur in Sonora (Mexico), but their ecology is largely unstudied. Although two subspecies of Gila Monsters are currently recognized (banded race—*H. s. cinctum*; reticulate race—*H. s. suspectum*), ongoing morphological and mtDNA analyses (Douglas et al., unpubl. data) do not support this simplistic division. With the exception of introduced exotic species (e.g., *Ctenosaura pectinata*; *Iguana iguana*; Conant and Collins, 1998), the Gila Monster is the largest (length and mass) species of lizard naturally occurring in the United States.

Populations of Gila Monsters persist in the vicinity of metropolitan areas experiencing rapid growth, such as Las Vegas, Nevada, USA, and both Phoenix and Tucson, Arizona, USA. Translocation of individual Gila Monsters found in or near houses is currently practiced by various agencies and individuals in the Phoenix and Tucson areas, although the fate of these animals is largely unknown. Translocation of large reptiles such as Gila Monsters is of special concern because they are top-order predators, feeding primarily on birds and mammals (Beck, 1990; Bogert and Martin del Campo, 1993); it is conceivable that their removal and release might have negative ecological impacts (Kjoss and Litvaitis, 2001; Shine and Koenig, 2001). Consequently, with support from the Heritage Program of the Arizona Game and Fish Department, we undertook a study of individuals with surgically implanted radio-transmitters to ascertain the consequences of translocation of "nuisance" Gila Monsters in the northeastern Phoenix Metropolitan Area.

2. Methods

2.1. Subjects

Subjects were obtained through calls from the general public when a "nuisance" Gila Monster was encountered by a resident in the northern Phoenix Metropolitan area and local agency personnel were notified (e.g., Arizona Game and Fish Department). We responded to the call, obtained the Gila Monster at the residence or from the agency personnel that had removed the animal, returned it to the laboratory for processing and surgery, and then released the animal at or near the site, or at some distance from the site if translocation was deemed necessary. Animals were generally released within 72 h of capture. A small number ($N=3$) of animals were retained in the laboratory until radio-transmitters could be obtained for implantation.

Following initial capture, subjects were transported to the Department of Life Sciences, Arizona State University West, where multiple body measurements were obtained, including length and width of head, snout-vent length (SVL), tail length and width, and body mass. Surgical implantation of radio-transmitters was performed within 48 h of capture (generally, procedures followed Beck, 1990). Subjects were anesthetized by placing their head into a clear plexiglass chamber containing air saturated with Isoflurane. A rubber collar around the chamber opening allowed a snug fit around the neck of the subject. They were assumed to be anesthetized when they failed to exhibit reflexes to light squeezing stimulation of their feet using a hemostat. An incision approximately 2 cm long was made longitudinally through the ventral integument and peritoneum just medial to the ribs, and a temperature-sensitive radio-transmitter (Model SI-2T, Holohil Systems Ltd.,164.000–164.999 MHz) was placed in the abdominal cavity. Radio-transmitters implanted in adult subjects had a mass of 11.4 g (always $<10\%$ of body mass); a single juvenile subject (20) was implanted with a smaller radio-transmitter (4.5 g). Radio-transmitters were anchored to a rib with a non-absorbable suture where the base of the antennae entered the transmitter case, and antennae were inserted subcutaneously from the abdominal cavity, extended anteriorly and dorsally, and anchored in the neck region. For subsequent identification, a passive integrated transponder (PIT) tag was also inserted in the abdominal cavity during surgery. The incision through the integument was closed with absorbable sutures and subjects were allowed to recover from anesthesia. Because Gila Monsters cannot be reliably sexed using external characteristics, prior to recovery from anesthesia, individuals were sexed by injection of sterile saline solution 20–30 mm posterior to the cloacal opening to evert a hemipenis. Within 48 h, subjects were released at either the point of capture, or at a translocation site. All subjects were recaptured at least once to monitor changes in mass, and status of surgical incisions.

All subjects were photographed; individuals were easily recognized by matching distinctive pigment patterns on the head and body to the photographs (confirmed by PIT-tag signatures). Subjects recaptured after battery failure (8–21 months) were returned to the laboratory, the radio-transmitter was surgically removed, and the subject released following recovery (Table 1).

2.2. Translocation

Subjects were translocated when the homeowner was anxious about the safety of pets or children, or both, and requested that the Gila Monster not be returned to the immediate vicinity. All subjects were released adjacent to appropriate refuges, either packrat nests or rodent burrows. Other subjects were translocated when the surrounding area was undergoing urban development ($N=15$). The remaining subjects were moved less than 200 m from their capture site, and considered "non-translocated" ($N=9$). All of these individuals were observed in the vicinity of their capture site within days of release.

Nine of 15 translocated subjects were released in open habitat away from homes but in the general vicinity (200–7688 m distances) of their original capture sites. The six remaining translocated subjects were released at the primary translocation site, a large (1206 ha) area of State Trust land in the center of the study area. This site was selected because it was the largest area of continuous, relatively undisturbed Sonoran Desert habitat in this region in which surrounding residents reported observing Gila Monsters in 1999 and 2000; many appropriate refuges (packrat nests, burrows) were available. The six subjects translocated to this site were all found in similar Sonoran Desert habitat with similar topography. Despite its acceptable appearance, it was nonetheless surrounded on all sides by paved roadways with significant traffic.

Table 1
Individual ID number (duration of tracking in months), capture date (CAPTURE), termination date (END), translocation DISTANCE (in meters), and apparent OUTCOME (Home = returned to capture site) for all Gila Monsters

ID (months)	CAPTURE	END	DISTANCE	OUTCOME
1 (14.5)	11 Apr 2000	27 Jun 2001	1657	Death
2 (24)	12 Apr 2000	5 Apr 2002	37	Home; tag removed
3 (16.5)	13 Apr 2000	1 Sep 2001	61	Home; tag down
4 (18.5)	13 Apr 2000	31 Oct 2001	136	Home; tag down
5 (17)	19 Apr 2000	27 Sep 2001	0	Home; tag down
6 (16)	24 Apr 2000	24 Aug 2001	240	Home; tag down
7 (16)	26 Apr 2000	1 Sep 2001	360	Home; tag down
8 (11.5)	16 May 2000	30 Apr 2001	937	Home; translocated
8 (1)[a]	30 Apr 2001	15 May 2001	9560	Lost
9 (19)[b]	31 Jul 2000	18 May 2002	169	Home; death
10 (12)[b]	31 Aug 2000	5 Aug 2002	136	Home; tag down
11 (13)	4 Mar 2001	12 Apr 2002	441	Home; tag removed
12 (15)	16 Apr 2001	31 Aug 2002	0	Home: end of study
13(15)	16 Apr 2001	31 Aug 2002	628	Home; end of study
14 (15)	23 Apr 2001	31 Aug 2002	582	Home; end of study
15 (2)	1 May 2001	27 June 2001	68	Home; death
16 (14)	12 May 2001	31 Aug 2002	49	Home; end of study
17 (1)	15 May 2001	1 Jun 2001	18 268	Lost
18 (1)	19 May 2001	1 Jun 2001	22 410	Lost
19 (3)	5 Jun 2001	1 Sep 2001	9845	Lost
20 (9)[b]	4 Jul 2001	15 May 2002	24 700	Tag down
21 (1)	9 Jul 2001	29 Jul 2001	7688	Lost
22 (11)	30 Jul 2001	31 Aug 2002	511	Home; end of study
24 (9)	26 Aug 2001	18 May 2002	270	Home; tag removed
25 (11)	31 Aug 2001	31 Aug 2002	419	Home; end of study

[a] Female 8 was translocated a second time.

[b] Some animals were retained in lab prior to release.

2.2.1. Data acquisition and analysis

Subjects with implanted radio-transmitters were located by an observer on foot using a hand-held antennae and receiver (Telonics TR-1) every 2–3 days from March through October, and every 3–5 days from November through February, 2000–2002. When an individual was located, general notes on behavior (e.g., basking, walking) and location (e.g., in a burrow) were recorded. Universal Transverse Mercator (UTM) coordinates were found for its position using a handheld Global Positioning System (GPS) unit (Garmin 12 XL). UTM coordinates were transferred into ArcView 3.2 Spatial Analysis software (Environmental Systems Research Institute, Inc), and movement patterns were analyzed using the Animal Movement extension (Hooge et al., 1999). Movement patterns were analyzed by year (2000, 2001) for home range area (ha), mean distance moved (m), total distance moved (m), and mean daily speed (m/day). Home range was estimated using 100% minimum convex polygon and kernel 95% contour intervals, as determined by ArcView. For kernel estimates of home range size, smoothing values were determined using least-squares cross-validation (Seaman et al., 1999). Because both measures of home range were highly correlated, only minimum convex polygon values are provided here. Statistical tests were two-tailed with ∝ of 0.05.

3. Results

Twenty-five Gila Monsters were processed during 2000 and 2001 (Table 1). Two of these were juveniles (20 and 23), and only one (20) was implanted with a radio-transmitter (23 was released untagged). Of the adult subjects, eight were males and 15 were females.

All ($N=18$) individuals released less than 1000 m from where they were first captured returned to the capture site vicinity in one to thirty days (Table 1). These individuals were thus classified as "non-translocated" for analysis of home range and mean daily speed parameters using movements and refuge use subsequent to successful homing. Because one individual that returned to its capture site in 2000 was translocated a second time in 2001 (female 8), seven individuals were classified as translocated (Table 2). Because of the potential of seasonal effects on home range size and mean daily speed, comparisons were restricted to within years (2000 and 2001), and statistical analysis was only possible with data from 2001 due to sample size restrictions (e.g., only one subject in 2000 was translocated more than 1000 m). Additionally, home ranges could only be calculated for a small number of translocated individuals ($N=4$) that were relocated on more than five occasions before they were "lost" (see below). There was no obvious homing behavior (e.g., straight-line or circular movements) exhibited by translocated subjects.

Table 2
Individual ID number (T = "non-homing translocation"), sex, snout-vent length in mm (SVL), home range in 2000 in hectares (HR 2000), home range in 2001 in hectares (HR 2001), and mean daily speed in meters (mds)

ID	SEX	SVL	HR 2000 (mds)	HR 2001 (mds)
1 (T)	M	250	121.9 (54.8)	95.1 (48.9)
2	F	285	3.5 (7.6)	9.2 (12.1)
3	M	300	44.9 (20.9)	6.5 (13.0)
4	F	240	4.2 (8.3)	28 (11.0)
5	F	265	3.1 (5.6)	4.2 (10.5)
6	F	335	55.9 (46.9)	36.6 (14.8)
7	F	305	6.3 (10.6)	6.7 (14.1)
8	F	308	67.6 (19.1)	7.3 (4.4)
8 (T)[a]	F	308	–	9.8 (34.0)
9	F	340	–	8.8 (8.4)
10	F	290	–	6.8 (7.1)
11	F	305	–	17.8 (8.1)
12	M	320	–	10.1 (6.7)
13	F	230	–	27.5 (16.8)
14	F	255	–	14.4 (9.5)
15	F	289	–	–
16	F	207	–	3.0 (5.2)
17 (T)	F	325	–	– (33.8)
18 (T)	M	258	–	–
19 (T)	M	280	–	190.2 (88.0)
20 (T)	F	180	–	15.4 (10.4)
21 (T)	M	250	–	8.4 (120.5)
22	M	230	–	17.6 (15.8)
24	M	235	–	5.5 (8.7)
25	F	270	–	1.8 (7.8)

[a] Female 8 was translocated a second time on 30 April 2001.

From 2000 to 2001 home ranges of non-translocated males ($N=4$) ranged from 5.5 to 44.9 ha, and non-translocated females ($N=14$) ranged from 0.25 to 67.6 ha. Many non-translocated subjects consistently used burrows near or under homes and other structures (e.g., utility boxes; Fig. 1). Mean daily speed of non-translocated males ranged from 6.7 to 15.8 m/day, and non-translocated females ranged from 4.4 to 46.9 m/day. Home range ($r=0.21$, $P=0.42$, $N=17$) and mean daily speed ($r=0.09$, $P=0.73$, $N=17$) were not significantly correlated with body size (SVL) in either males or females that were classified as non-translocated in 2001. Given the absence of significant differences between males and females, and that sample size was small, data for the sexes were pooled for comparison of home range and mean daily speed in 2001.

Although home ranges of non-translocated individuals ranged from 1.8 to 36.6 ha in 2001, and those of translocated individuals ranged from 8.4 to 190.2 ha, this difference was not statistically significant (Mann–Whitney $U=14$, $P=0.073$, $N=21$; Table 2). The home ranges of the two translocated adult males followed for at least one month (1 and 19) were especially large (95.1 and 190.2 ha in 2001; Fig. 2a); most translocated individuals were followed for an insufficient period (less than one month) to obtain a meaningful home range

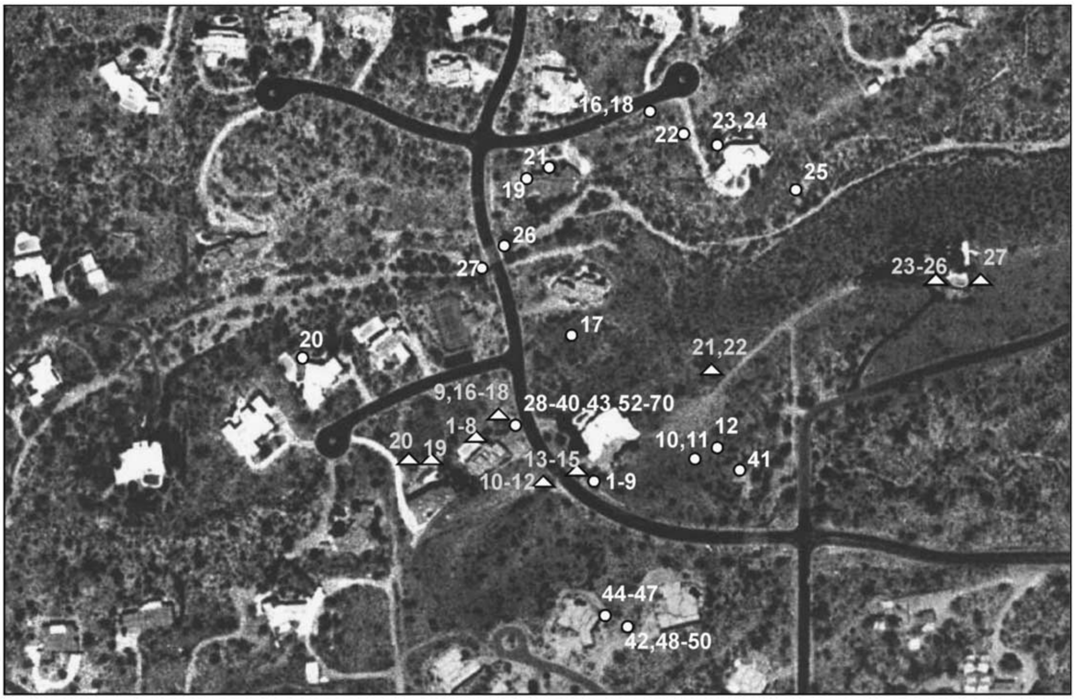

Fig. 1. Aerial photo of the town of Carefree, Maricopa County, Arizona, showing movements and refuge use of two nontranslocated female subjects (9 = circles; 10 = triangles) in 2001. Note refuges used near homes and roadways. Multiple use of the same refuge denoted by numerical sequences (e.g., 52–70 for female 9 represent overwintering site use without apparent movement).

estimate before they were lost. The fate of lost individuals could not be determined, in spite of extensive searches on all surrounding roadways. A small plane was used in an attempt to detect signals from long distance movements (up to 15 km), but proved unsuccessful. In the absence of transmitter battery failure (transmitters were exceptionally reliable initially; none failed within 6 months of implantation), it is reasonable to assume lost individuals died on roadways surrounding the translocation site and the transmitters were destroyed. A single radio-transmitter placed in the body of a Gila Monster found dead was non-functional after only five hits by a passenger car, suggesting they would not last long on a well-used roadway.

Mean daily speed (MDS) of non-translocated individuals ($N = 17$) ranged from 4.4 to 16.8 m/day while that of translocated individuals ($N = 5$) ranged from 10.4 to 120.5 m/day in 2001 (Table 2). Translocated individuals (average MDS = 60.3 m/day) exhibited a significantly higher MDS (Mann–Whitney $U = 8$, $P = 0.007$) than non-translocated individuals (average MDS = 10.24 m/day). For example, female 8 was initially translocated 937 m; she returned to her capture site (home) within 1 month. Over the next 11 months, she exhibited a home range of 67.6 ha, and a MDS of 19.1 m/day. After being removed from a residence on two occasions in spring 2001, at the request of the home owner she was translocated 9560 m to the translocation site. She was lost within 1 month, and during this time exhibited a MDS of 34.0 m/day.

Only two translocated individuals were followed for two seasons. Male 1 was translocated 1,657 m, and exhibited a MDS of 54.8 m/day in 2000 (Fig. 2a), and 48.9 m/day in 2001 post emergence (i.e., March–June). Hence, his MDS in 2001 was not reduced relative to that exhibited in 2000 immediately following translocation. By contrast, female 20 was translocated 24,700 m; immediately after release in late summer, she exhibited a home range of 15.4 ha, and a MDS of 38.68 m/day in the first month following release. During fall and early winter, she moved relatively little, and for all of 2001 her home range was 15.4 ha (MDS = 10.4 m/day). When she emerged from hibernation in March, 2002, she exhibited a home range of only 0.01 ha, and a MDS of only 0.40 m/day. Due to her small size (SVL = 180 mm), it is possible that she had more successfully adjusted to the translocation site than the only other individual that we were able to follow after overwintering at a translocation site. However, she was the only subject under 300 mm SVL that did not gain in mass across seasons, and it is conceivable that she was declining in health as result of her initially high movements subsequent to translocation. Unfortunately, her radio-transmitter failed after 2 months of activity in the spring (March–May, 2002).

During this study three individuals died; two were non-translocated individuals apparently struck by automobiles (9 and 15) and the other was a translocated subject. This male was found dead, apparently killed and eaten by a mammalian predator, 14 months post-release (Sullivan et al., 2002).

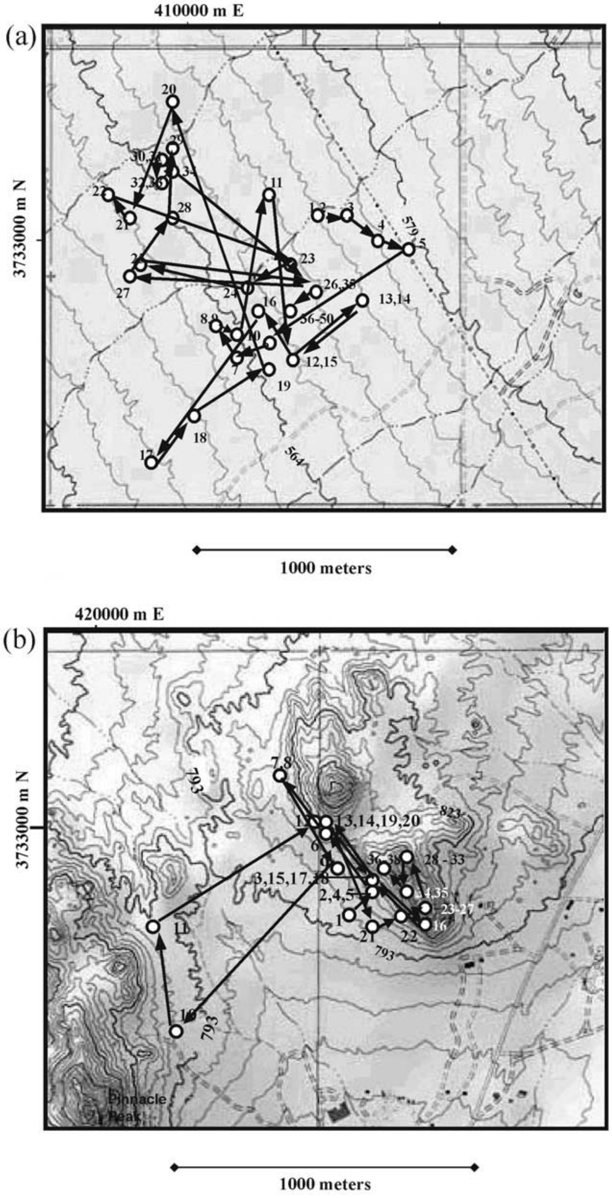

Fig. 2. (a) Movements of translocated male subject (1) at the primary translocation site in 2000; (b) movements of nontranslocated male subject (3) during 2000. Both individuals were followed from late April through December: male 1 used 29 refuges and male 3 used 17 refuges during the 8 month period.

4. Discussion

4.1. Gila Monsters and translocation

Our results indicate that short distance translocations are ineffective as a means of removing Gila Monsters from areas of conflict with home owners. Numerous Gila Monsters that we moved less than 1000 m were encountered (and tolerated) by homeowners, and regularly used refuges near original capture sites following translocation. Clearly, Gila Monsters can successfully return if displaced a short distance; others have documented a direct relationship between translocation distance and return rate in nuisance mammals (e.g., Blanchard and Knight, 1995). If the goal of translocating Gila Monsters is their permanent removal from an area due to human conflict, translocation distance must exceed 1 km.

Gila Monsters translocated more than a kilometer did not return to the original capture site (home), at least in the urbanized desert environment we examined. Unfortunately, all adult subjects that failed to return were lost or died, suggesting that translocated individuals do not readily tolerate a novel environment. Translocated Gila Monsters exhibited higher mean daily movements, almost five times higher than non-translocated individuals. Similarly, Reinert and Rupert (1999) found that translocated timber rattlesnakes moved almost three times as far each day as non-translocated individuals, and Nowak et al. (2002) documented increased movement rates for translocated Western Diamond-backed Rattlesnakes. Increased activity, especially for the typically sedentary Gila Monster (Beck and Lowe, 1994; Beck et al., 1995) might entail significant energetic and thermoregulatory costs, as well as predation risks. The only Gila Monster less than 300 mm SVL that did not increase in mass across seasons was a translocated female (20). The high activity levels of translocated Gila Monsters that we observed may have led to mortality due to predation (e.g., male 1). Reinert and Rupert (1999), Plummer and Mills (2000), and Nowak et al. (2002) documented that translocated snakes in their respective studies differed significantly in mortality rates in relation to release status: translocated individuals had higher mortality. In our study, we suspect that the translocated Gila Monsters that were lost died on roadways surrounding the translocation sites, although we have no direct evidence of this.

Although two non-translocated Gila Monsters with radio-transmitters died as a result of being struck by automobiles, most survived for an extended period, often in close proximity to roadways and homes (Fig. 1). The survivorship of the non-translocated Gila Monsters in the Phoenix urban–desert interface was somewhat surprising given high levels of human activity (e.g., construction, roadways). Parent and Weatherhead (2000) also found that Massasauga were apparently relatively tolerant of human disturbance. Our Gila Monsters were potentially exposed to higher prey densities than might have otherwise been available in the surrounding desert environment. Quail, dove, and cottontail rabbits, are especially abundant in many desert-urban interface environments, even in dry years in which little reproduction occurs among these species in the surrounding desert (B. Sullivan unpubl.).

4.2. Translocation as a conservation tool

We documented significantly increased movement rates for translocated Gila Monsters. Although high activity rates of translocated individuals in novel environments are expected, other effects of translocation require consideration. Many of the non-translocated Gila Monsters that we radio-tracked used the same refuge repeatedly over 12–18 months of observation (Figs. 1 and 2a). Translocation could have negative consequences depending on the degree to which individuals rely on particular refuges for escape from predators, to regulate body temperature or to maintain water balance. Thermoregulatory behavior by ectothermic vertebrates like Gila Monsters might be especially disrupted by a translocation event. Additionally, although there is a general perception that birds and mammals are more likely than reptiles to have structured or relatively complex social systems, and hence be negatively impacted by translocation, it is now appreciated that many reptiles exhibit complex social relationships (e.g., Gardner et al., 2001). Longitudinal study of translocated individuals is necessary to determine the consequences of this conservation technique, but it is clear that the notion that animals can be ‘‘rescued’’ by simply moving them from one area to another is naive and potentially dangerous to the individual and both resident and host populations (Pietsch, 1994; Shine and Koenig, 2001; Seigel and Dodd, 2002).

Translocation can also have significant ecological consequences at the population and community levels. For example, Gila Monsters are one of several top-order predators (young birds and mammals are their primary prey; Beck, 1990) in desert environments. The loss of but a few individuals could negatively impact ecological interactions among remaining species (Kjoss and Litvaitis, 2001; Shine and Koenig, 2001). Translocations also provide opportunity for disease introduction for resident populations (Cunningham, 1996; Shine and Koenig, 2001; Seigel and Dodd, 2002). Furthermore, genetic consequences of translocation requires careful consideration (Stockwell et al., 1996; Whiting, 1997), and concerns have centered on the viability of re-established populations (Stockwell et al., 1996; Madsen et al., 1999). However, most reptile translocations in urbanized desert areas occur over short distances; hence, spread of diseases or parasites is likely minimal (Cunningham, 1996), as are potential negative genetic consequences.

In conclusion, our translocation study of Gila Monsters is important in that it addresses a current urban management problem of a top-order reptilian carnivore that is large, venomous, and protected by law. The negative results of our translocation study place time and monetary constraints on agency personnel concerned with the fate of nuisance animals; there is a clear need for a more satisfactory conservation mechanism. Despite this dilemma, we are optimistic that public education by agencies and scientists working on Gila Monsters can alter negative opinions, and that this species can be portrayed as an extraordinary low risk threat to humans minimizing the need for translocation. Our own interactions with homeowners, for example, demonstrated high interest in the safety and well-being of individual Gila Monsters.

Acknowledgements

This work was supported by a Heritage Fund Grant from the Arizona Game and Fish Department. Dale DeNardo assisted with surgical efforts and IACUC approval. Rob Bowker, Paul Hamilton, Shannon Hoss, Jamie Howard, and Ron and Devon Rutowski assisted with some field observations. Daniel, Elizabeth, Keith and Justin Sullivan provided considerable support; Keith was especially helpful in radio tracking. The Arizona Herpetological Association, most notably Bill Sloan and Russ Johnson, were helpful in coordinating interactions with homeowners. The staff of the Four Seasons Resort (Scottsdale) coordinated captures and releases of Gila Monsters on numerous occasions. Randy Babb, Dan Beck, Mike Demlong, and Roger Repp deserve special thanks for many discussions about Gila Monster natural history. Last, the many residents of northern Phoenix, Scottsdale and Carefree deserve thanks for tolerating researchers as well as Gila Monsters in their neighborhoods.

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Journal of Herpetology, Vol. 24, No. 1, pp. 54-68, 1990

Ecology and Behavior of the Gila Monster in Southwestern Utah

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ABSTRACT.—**Activity patterns, behavior, food habits, and thermal biology were investigated by radiotelemetry in a population of banded Gila monsters in southwestern Utah. Twenty-seven Gila monsters were observed within a 2 km^2 area. They fed on eggs and young mammals taken from nests. Quantities as large as 210 g, eaten in a single meal, did not appear to be envenomated. Activity peaked between late April and mid June, from 0800 to 1200 h. Distances traveled during activity bouts averaged 210 m (approximately 50 min), although individuals occasionally traveled over 1 km. Lizards were active on less than 10 days/month during their 90-day activity season, spending over 95% of their time below ground in shelters. This low energetic investment to activity is contrary to traditional descriptions of activity of lizards that forage on patchy prey. Gila monsters had a relatively low activity temperature ($\bar{x}$ = 29.4 C) and at rest spent over 83% of the year at body temperatures of 25 C or below. Lizards occasionally basked near shelters in the spring. Several shelters were reused, some by more than one lizard, occasionally concurrently. Intraspecific interactions, including male combat, observed near shelters suggest that these helodermatids have a structured social system. Analysis of a 3-h fight between two large males revealed similarities with varanid lizard and crotaline snake combat, as well as similarities to combat in captive helodermatids.**

Heloderma suspectum and *H. horridum* are the only extant members of the Helodermatidae, a family whose fossil record extends from the late Eocene of France and the late Cretaceous in North America (Pregill et al., 1986). Their current geographic distribution is limited largely to hot desert regions of the southwestern United States and desert, thornscrub, thornforest and tropical deciduous forest regions of western Mexico and Guatemala (Campbell and Vannini, 1988).

The venom and other unique qualities of helodermatids have interested herpetologists for many years (Bogert and Martín del Campo, 1956), but because these lizards rarely appear on the surface, field study over extended periods has been difficult. Recent work in Arizona has shown *H. suspectum* to be a secretive diurnal predator with a relatively low activity temperature, and a dietary specialization on eggs and young in vertebrate nests (Porzer, 1981; Jones, 1983; Lowe et al., 1986).

Finding nests, a widely distributed food source, should require a "widely searching" foraging mode (Huey and Pianka, 1981). Previous studies of lizard energetics have shown that "widely searching" predators allocate a greater portion of their respiratory energy to activity than to "sit and wait" predators (Anderson and Karasov, 1981; Huey and Pianka, 1981; Andrews, 1984; Nagy et al., 1984). One might predict that *Heloderma* would have similarly high activity costs during its activity season, yet little has been reported on actual distances traveled by free-ranging Gila monsters over extended periods, or on their energetic investment in activity. Their ability to take large meals and low energy demand while inactive (Beck, 1986) might make frequent searching for food unnecessary.

Here I present results of a 3-yr field study of *Heloderma suspectum cinctum* at the northern periphery of its range in southwestern Utah. I provide information on activity, food habits, habitat use, thermal biology, and behavior that sheds light on the social behavior, ecology and evolution of this species. I describe male-male aggressive behavior and discuss its physiological implications.

METHODS

Study Area.—The study site, a N-S oriented canyon, is in a Mojave/Great Basin Desert transition area near St. George, Washington County, Utah. Three km north of its mouth, the canyon opens into a sandy valley, 0.8 km wide and 1.7 km long, bounded by Navajo Sandstone cliffs to the W, N and E. Portions of the cliffs are capped with basaltic lava flows. Lava and sandstone boulders, strewn along the slopes of the cliffs and valley floor, provide shelters for *Heloderma*. The valley floor is largely composed of reddish-pink sand dunes deposited from the surrounding cliffs, and is dissected by several small washes. Considerable foraging activity

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occurs on these sandy areas. Elevation varies from 940 m at the valley floor to 1000 m along the canyon rim. The study area encompasses approximately 200 ha. Dominant vegetation includes creosote bush (*Larrea tridentata*), sand sage (*Artemisia filifolia*), and blackbrush (*Coleogyne ramosissima*). Annuals can be abundant from April through mid June.

Thermographs housed in a weather station installed near a center of Gila monster activity on the study site continuously recorded temperatures at 1.5 m above and 5, 25, and 75 cm below the surface. Additional substrate and ambient temperatures were recorded with hand held Shultheis and Tel-Tru (Germanow-Simon Co.) thermometers.

Study Procedures.—Preliminary fieldwork was conducted from 5 May–16 June, 1982, followed by two seasons utilizing radiotelemetry. Five Gila monsters captured on the study site were implanted with radio transmitters in May and June 1983, and monitored, usually daily, through September. Transmitters with fresh batteries were reimplanted into two lizards in October; these were monitored periodically through winter and spring, 1984. Daily observations resumed in mid April and continued through mid June 1984.

Gila monsters were located by following trackways in sandy areas. Animals were measured (snout-vent length [SVL], tail length, and tail circumference), placed in cloth bags and weighed (nearest 2 g) with Pesola spring scales. Lizards were toe-clipped for identification, and usually released shortly after capture. Fecal samples were collected from lizards that were retained. Body temperatures were determined with a Shultheis thermometer inserted 5 cm into the gut through the cloaca, and with radio transmitters.

Temperature-sensing radio transmitters were used to monitor lizard locations and to record body temperatures. The radio transmitters (IMP-200-L, Telonics) were hermetically sealed, paraffin-coated units weighing 23 g (6 × 2 cm). They had a battery life of 8–10 mo with a transmission range of 0.3 to 5.8 km, depending upon the terrain. Transmitter pulse rates varied with temperature; they were calibrated in a water bath and were accurate to within ±0.3 C.

Lizards were anesthetized with Ketelar (ketamine HCL) prior to radio implantation surgery. A transverse incision was made through the ventral surface to the right of the midline, 25–30 scale rows anterior to the vent. Transmitters were soaked in isopropyl alcohol then in Ringer's solution before implantation in the peritoneal cavity. Incisions were closed with gut suture and coated with Colotion. Lizards were released at the point of capture within one week after surgery. Transmitters were removed through an incision adjacent to the previous one using similar surgical procedures. Radio-implanted lizards were monitored with a portable receiver (Telonics, TR-1) and hand-held directional antenna.

Foraging paths, sequential relocations and shelters were marked on aerial photos of the study site. Shelters were marked with cairns for future identification. Several temperature samples were taken from each radio-equipped lizard, usually daily; time and behavior of the lizard (active, basking, or inside shelter) were recorded for each temperature sample.

Gila monster trackways in sandy areas were examined daily. Marked individuals left characteristic trackways that could be identified up to several h later. Distances traveled were paced off; date, location, and areas visited by lizards were recorded and marked on maps. Rate of travel was determined by timing Gila monsters; the actual (not straight line) distances traveled were measured and divided by time.

Data on diet were gathered by observing foraging, following trackways and noting nests invaded, and examining feces. Prey remains in feces were identified using a mammal guard hair key (Mayer, 1952) and a reference collection.

Home ranges were calculated for lizards with a minimum of 15 sightings over 10 mo using the convex polygon method (Jennrich and Turner, 1969; Rose, 1982). Means are followed by ±1 SD.

RESULTS AND DISCUSSION

A total of 27 Gila monsters was captured, marked and measured on the 2.0 km^2 site (Appendix 1). Most (52%) were large adults, >320 mm SVL. Thirteen lizards (48%) were over 325 mm SVL, a size that Bogert and Martín del Campo (1956) thought *H. suspectum* rarely attains. Only one immature (221–260 mm SVL) and no juveniles (<220 mm SVL) were observed during the study.

Some of the Gila monsters on the study site had been marked and measured between 1975 and 1977 (Coombs, 1977), so data on growth for periods of up to 7 yr were obtained. Growth in body length was relatively slow in adults, averaging 4.8 mm/yr in individuals initially under 300 mm SVL, and 2.1 mm/yr in larger lizards (Table 1). Growth rates of 7–10 mm/yr have been reported for captive adult Gila monsters (Bogert and Martín del Campo, 1956; Tinkham, 1971).

Food Habits.—The diet of *H. s. cinctum* in Utah, based on four direct observations and 20 fecal samples, consists of infant cottontails (*Sylvilagus auduboni*, 42% of observations), desert tortoise (*Xerobates agassizi*) eggs (29%), young ground

FIG. 1. Adult male *Heloderma suspectum cinctum* eating a young 40 g cottontail (*Sylvilagus auduboni*) from a nest in June, 1983. Four rabbits were swallowed alive without envenomation.

squirrels (*Ammospermophilus leucurus*, 8%), young rock squirrels (*Spermophilus variegatus*, 8%), mourning dove (*Zenaida macroura*) eggs (8%), and carrion (young *Dipodomys merriami*, 4%). Large quantities can be ingested during a single feeding. A 650 g lizard consumed 210 g of young cottontail rabbits at 1100 h on 27 May, 1983, and another Gila monster (640 g) consumed 4 young rabbits (160 g total) at 1115 h on 12 June, 1983. On 3 June 1982 at 1230 h, a Gila monster excavated and consumed a desert tortoise nest of four eggs. The eggs were broken by the lizard and their contents lapped up along with a considerable quantity of sand.

On each occasion the lizards spent 5-15 min excavating the nests, and all young or eggs inside were consumed. This feeding behavior contrasts with that reported in northwestern Arizona for *H. suspectum*, which consumed an average of only 46% of eggs available at each of 24 Gambel's quail nests (Jones, 1983).

Prey eaten by Gila monsters in the field were not obviously envenomated. The young cottontails, 35-45 g each, were swallowed without the characteristic chewing motions of envenomation, even when the rabbits were struggling lightly (Fig. 1). Pregill et al. (1986) suggest that venom injection by *Heloderma* is an adaptation for preying on large, bulky vertebrates in periodically cool environments, and that the skull morphology evolved from use of the massive jaws to kill and partially process large, defenseless prey (but see Greene, 1988). My field observations of Gila monsters eating relatively bulky mammalian prey do not support the hypothesis of a feeding role for the venom apparatus. As discussed by Lowe et al. (1986), the venom and delivery system of extant helodermatids most likely serves a primary role in defense.

Thermal Biology.—Mean monthly body temperatures of Gila monsters, excluding those during activity, ranged from 28.0 C in July 1983, to 12.3 C in late December 1983 (Fig. 2). When a lizard was inside a shelter, its body temperature typically fluctuated less than 1.0 C over a 24 h period.

Gila monsters spent more than 83% of the year at body temperatures of 25 C or less, and over 50% of the year at or below a body temperature of 20 C (Fig. 2). Body temperatures of lizards resting inside shelters were significantly correlated with surrounding air and soil temperatures (r^2 = 0.36, 0.17, 0.58, and 0.36 for air temperature at 1.5 m, and soil temperatures at 5, 25, and 75 cm below the surface, respectively). Winter body temperatures ranged from 11.3-15.2 C. These fall within the range experienced by other hibernating reptiles (1-15 C; Gregory, 1982). Soil temperatures at 75, 25, and

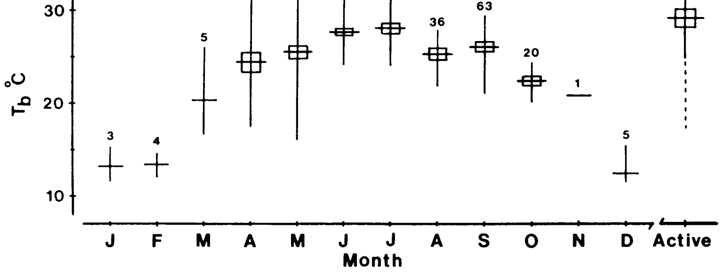

FIG. 2. Body temperatures of Gila monsters by month while at rest inside shelters and, on the far right of the figure, during surface activity. Dashed line indicates body temperature experienced during fighting, but not in other surface activities. Horizontal lines indicate means, vertical lines indicate ranges, and boxes indicate ±2 SE of the mean. Numbers above indicate sample sizes.

TABLE 1. Growth of free-living Gila monsters in Utah. Pre-1980 data are from Coombs (1977, and unpubl. data).

Lizard number	Initial date	SVL (mm)	Final date	SVL (mm)	Months elapsed	Growth (mm)	Growth rate (mm/yr)
PC8	Jun 1977	295	May 1982	330	59	35	7.1
PC6	Jun 1975	287	May 1982	331	83	44	6.4
PC18	Jun 1976	310	May 1983	343	83	33	4.8
PC3	Jun 1975	290	May 1982	317	83	27	3.9
PC14	Jun 1982	343	Jun 1984	348	24	5	2.5
PC4[a]	Jun 1976	291	May 1980	298	47	7	1.8
PC10	Apr 1976	335	May 1978	338	25	3	1.4
PC9	Jun 1976	339	Jun 1982	345	71	6	1.0
PC20	May 1975	355	May 1982	360	84	5	0.7

[a] Lizard PC4 lost 63% of its tail in 1977, which may have curtailed its growth rate.

5 cm depth were 7.0–15.3 C, 2.0–16.5 C, and −2.5–30.5 C respectively, between December 1983 and March 1984. Air temperatures ranged from −8.5 to 26 C during the same period.

Because Gila monsters are inactive for such long periods, thermal biology during such times may play an important role in their energetics. Helodermatids have unusually low metabolic rates (Beck and Lowe, unpubl. obs.), and the Q_{10} for metabolic rate between 20 and 25 C is 2.9 for *H. s. cinctum* (Beck, 1986). Reduced metabolic rate at low body temperatures presents a significant energy saving during periods of inactivity and/or reduced body temperature.

Body temperature during activity ranged from 17.4–36.8 C (mean of 29.3 C ±0.51, N = 41; Fig. 2). The lowest activity temperature (17.4 C) occurred during an aggressive interaction at an ambient temperature below 12 C. The lowest body temperature during normal foraging activity was 24.1 C; the activity range for this species is probably closer to 24.1–36.8 C. Activity occurred between 10.0–34.0 C ambient temperature and 20.5–32.0 C substrate temperature. Environmental temperatures correlate less strongly with body temperatures during activity ($r^2 = 0.11$ and 0.22 for ground surface and air temperature, respectively) than with body temperatures while inside shelters. Activity temperatures observed in this study indicate that, in comparison with other lizards (Brattstrom, 1965; Avery, 1982), the Gila monster has a relatively low activity temperature range, especially for a diurnal, desert lizard (Lowe et al., 1986). Other workers have reported similar activity temperatures for *H. suspectum* in Arizona and Utah (Schwartzman and Ohmart, 1976; Coombs, 1977; Porzer, 1981; Lowe et al., 1986).

Occasional basking behavior was observed at shelters from March through early May. A lizard typically exited within the first h after sunlight hit the shelter entrance and pressed the ventral surface against the ground, flattening the body. It entered and exited the shelter several times throughout the morning (Fig. 3). One animal observed for several days in late April and early may 1984 maintained a mean body temperature of 28.5 C (±0.2 C, N = 147) during basking periods, despite considerably lower environmental temperatures (Fig. 3). Basking behavior did not precede foraging or follow feeding, but some interesting intraspecific interactions occurred at this time (see below). With the onset of hotter weather in mid May, basking became much more rare.

Shelters.—All shelters used by Gila monsters were in rocky areas. Of 79 shelters, 59% were in loose Navajo Sandstone and 41% were on basaltic lava slopes or flows. Some animals in these black lava areas show considerable color matching to the darker habitat background (Beck, 1985). Most shelters were natural cavities, at times slightly modified by digging of the resident lizard. Tortoise (*Xerobates agassizi*) shelters and woodrat (*Neotoma lepida*) mounds (8% and 10%, respectively) were also used as shelters. Sixty-seven percent of shelter entrances faced E, SE, or S; the few facing NW or NE (2%) were used only during June and July. Four shelters used for overwintering faced S.

One shelter in a lava flow was excavated in mid September, 1983. The lizard was 1 m below the surface and 2 m from the shelter entrance. Based on soil temperatures and radio-implanted animals, lizards were estimated to be 1.0–1.5 m below the surface in shelters used during the winter (late November through mid March).

Fifteen shelters (19%) were reused, five by more than one lizard and three by two or more concurrently. During May and June 1982, one shelter was used by at least six Gila monsters. This shelter is in an area where considerable activity has been observed since 1975 (Coombs, 1977). Many lizards return to this area in late April and early May. Communal "dens" were not used for overwintering.

Home ranges of two males and one female with sufficient relocation data were 66.2, 32.6,

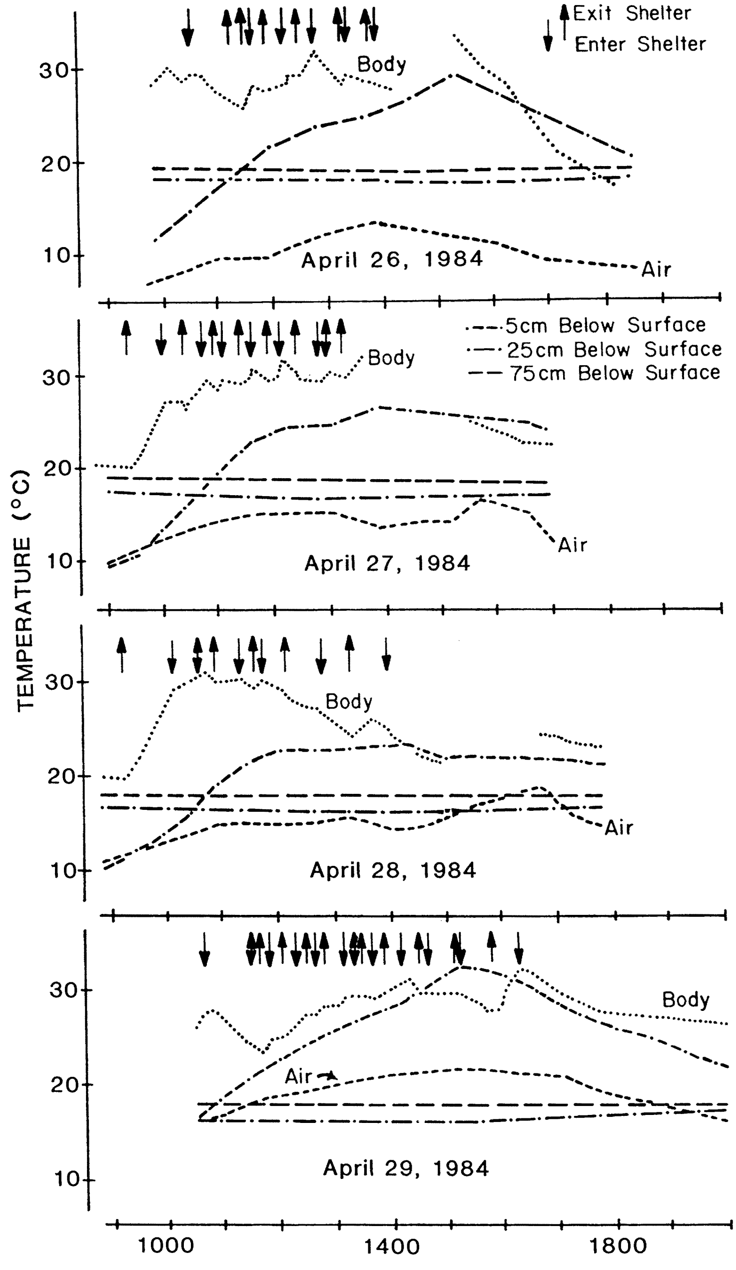

FIG. 3. Thermal relationships of a Gila monster while basking during late April, 1984. Arrows indicate entry and exit of the lizard into and out of shelter; double-sided arrows indicate that the lizard exited and re-entered the shelter within a 5 min period.

and 5.6 ha, respectively; their sequential shelter use is shown in Fig. 4.

Activity Patterns and Energetics.—Gila monsters are largely diurnal, not nocturnal as earlier believed (Bogert and Martín del Campo, 1956; Behler and King, 1979; Avery, 1982). Sixty-eight percent of the activity on the Utah study site occurred between 0830 and 1230 h (Fig. 5). In other parts of its range *H. suspectum* is also largely diurnal (Lowe et al., 1986), although nocturnal activity does occur. In southern Arizona *H. suspectum* is predominantly diurnal from March through May, crepuscular from June through September, and diurnal again from October

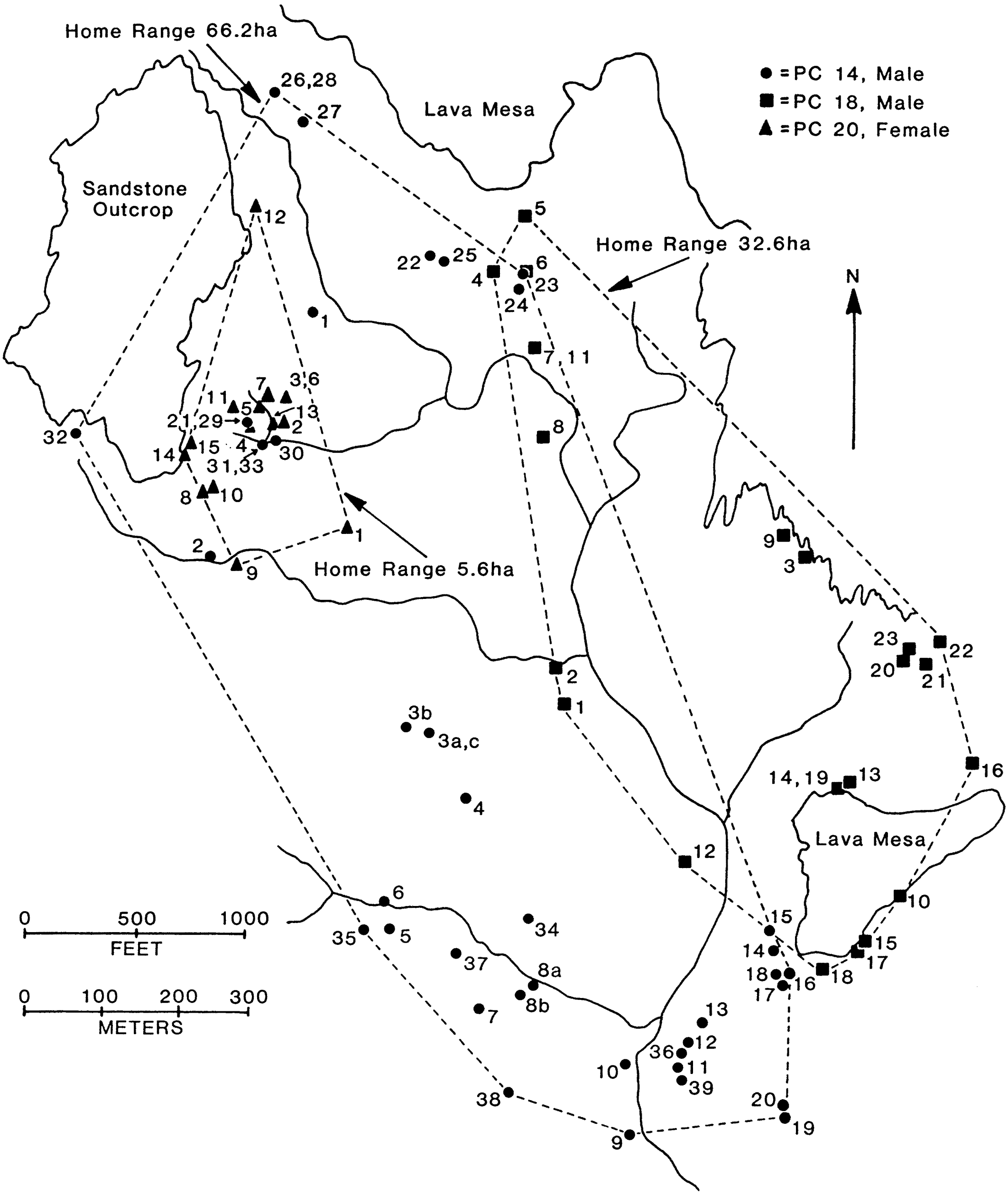

FIG. 4. Sequential shelter use by three Gila monsters on the Utah study site. Dates specific shelters were used, corresponding to the numbers in the figure, are given in Appendix 2.

through November (Lardner, 1969). Porzer (1981) and Jones (1983) reported crepuscular activity in *H. suspectum* in southern and northwestern Arizona, respectively.

Sixty-four percent of activity on the study site occurred from late April to early July (Fig. 6), and 77% of the total distance traveled by Gila monsters was recorded during that time. Gila monsters near Tucson, Arizona exhibited a similar activity peak during spring and early summer; from 1959–1964, 64% of surface activity (based on time of collection) was observed between mid March and mid June (see Fig. 5 in Lardner, 1969).

Radio-implanted lizards were active on an average of 9 days/mo during the 90-day activity season between mid April and mid July (Fig. 7). The maximum number of days/mo that any

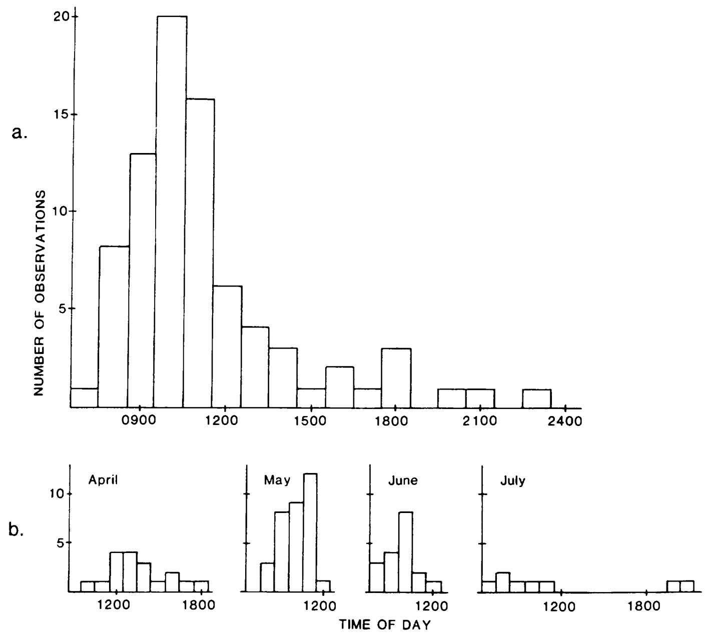

FIG. 5. Hourly distribution of Gila monster activity observed on the study site for all months combined (a) and by months of the activity season (b).

lizard was surface-active was 14, during June 1983. Later that summer (August-September) the same lizard remained at a single shelter for nine consecutive weeks with no detectable above-ground movements.

Above-ground travels of Gila monsters ranged from short trips of a few m around shelter entrances to journeys of more than 1 km (mean = 213 ± 13 m, N = 150; Fig. 8). Rate of travel averaged 0.25 km/h ± 0.03 (N = 10), with a duration of approximately 51 min for an average activity bout. The greatest distances traveled by any lizard during the activity season were: 1190 m between 15-30 April (lizard PC14); 3555 m during May (PC14); 3150 m during June (PC18); and 2000 m between 1-15 July (SC2) (Fig. 9). Summing these distances gives a maximum of 10.6 km traveled during the activity season. This value probably overestimates the

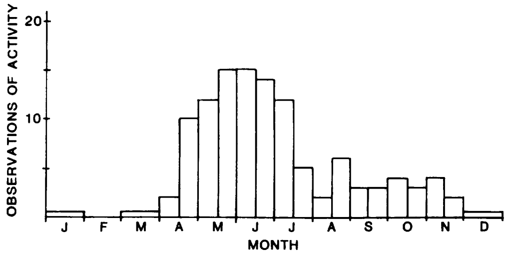

FIG. 6. Mean biweekly activity observed on the study site based on trackway and telemetry data from 5 radio-implanted and 13 marked *Heloderma suspectum* during 1982, 1983 and 1984.

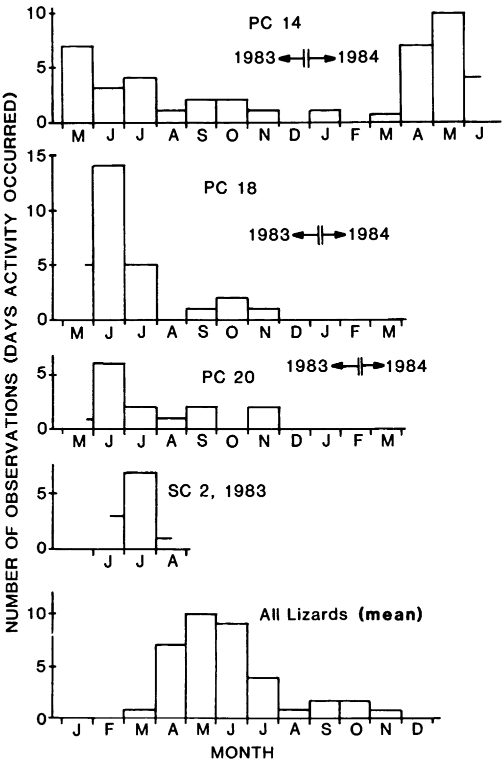

FIG. 7. Number of days radio-implanted Gila monsters were active during months that they were monitored.

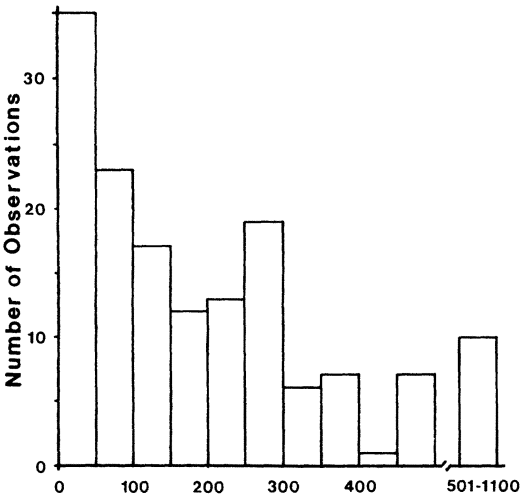

FIG. 8. Frequency distribution of minimum distance traveled during activity bouts by *H. suspectum*, $\bar{x} = 210$ m.

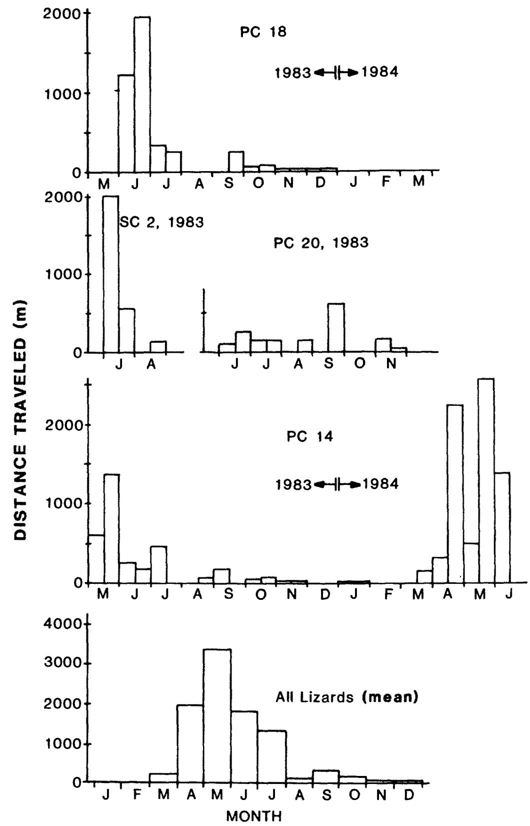

FIG. 9. Distance traveled by radio-implanted lizards during biweekly periods. Mean distance traveled per month is shown in histogram at bottom.

actual distance traveled by individual Gila monsters on the study site because it is based on the greatest distances traveled by any radio-equipped lizard during the activity season. I use it as an estimate of surface activity here because some activity may have gone unrecorded (e.g., trips where lizards returned to the same shelter), since lizards were not monitored 24 h/day. Given that 10.6 km represents 64% of annual surface activity, my estimate for the yearly distance traveled by a Gila monster on the study site is 10.6 km/0.64, or 16.6 km/yr. Assuming an average speed of 0.25 km/h, the estimated time spent in surface travel is 66.4 h/yr.

I observed Gila monsters digging in their shelters on a few occasions, and digging into reptile and mammal nests while foraging. One animal dug inside its shelter for a total of 7 h during late April and early May, 1984. The contribution of digging to the activity budget of the Gila monster is probably significant, but was not quantified in this study.

Heloderma suspectum specializes on the young and eggs in vertebrate nests, prey that are widely distributed in space. This requires search of a relatively large area, a foraging mode usually described as "widely searching" (Huey and Pianka, 1981). Studies on other lizards have shown that widely-foraging species have higher activity costs than do "sit and wait" predators, which typically wait for mobile prey to come within appropriate striking distance before initiating ambush and pursuit (Anderson and Karasov, 1981; Huey and Pianka, 1981; Nagy et al., 1984). Lizards in this study occasionally traveled long distances, up to 1 km, while searching for prey (nests). Energy demands increased to 1.5–3 times over resting levels (Beck, 1986). Such energy expenditures match those reported in other widely searching lizards during their activity periods (Anderson and Karasov, 1981; Huey and Pianka, 1981; Nagy et al., 1984). Activity was infrequent however, and large meals were eaten.

During the activity season, Gila monsters spend more than 97% of the time in shelters, and allocate less than 13% of their maintenance energy budget to surface activity (Beck, 1986). The energetic costs of searching for food are more than offset by long periods spent inactive. Thus, in terms of total time and energy allocated to activity during its activity season, the Gila monster ranks below "sit and wait" lizards, which allocate 25–35% of maintenance energy (respiration) to activity (Anderson and Karasov, 1981; Huey and Pianka, 1981; Nagy et al., 1984). Reptiles that search their environment for each prey item can have low activity costs if activity bouts are infrequent and large meals are eaten. The assumption that a "widely searching" foraging mode requires a high energetic investment in activity is valid for smaller species that

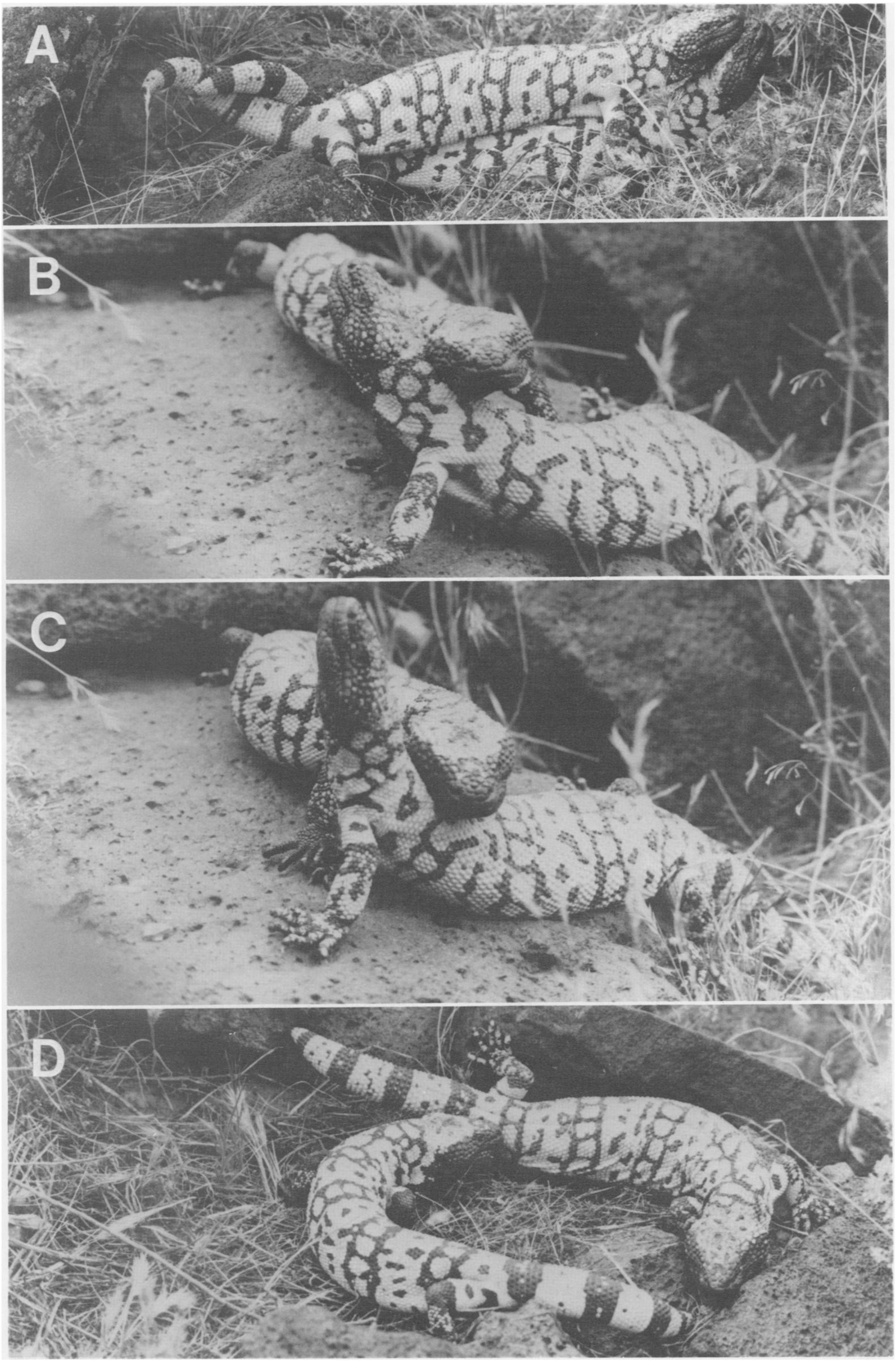

FIG. 10. Behavioral sequences during combat as described in text: (A) Dorsal Straddle; (B) Lateral Head Shove while other lizard responds with Neck Arch; (C) Head Raise; (D) Circling.

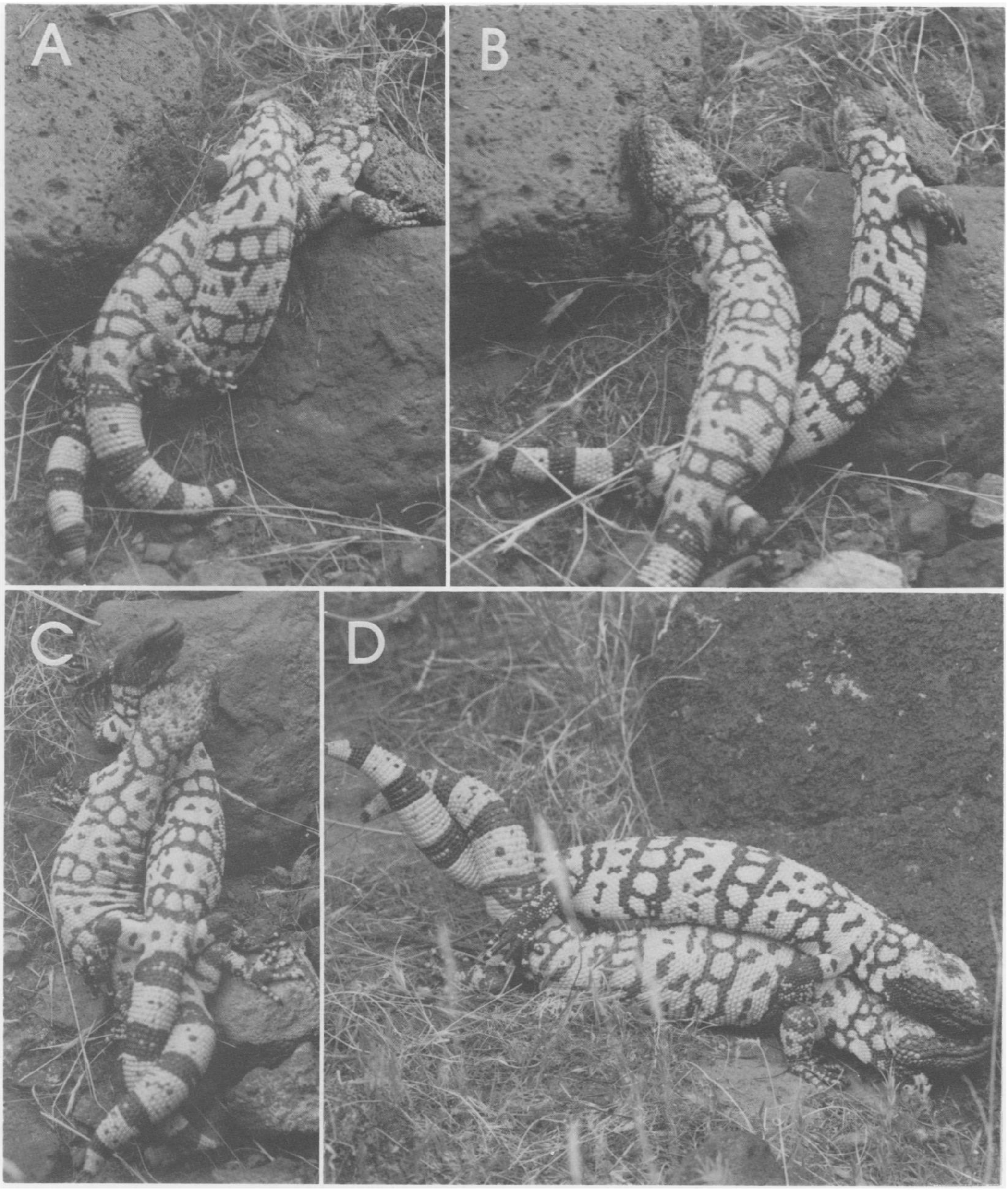

FIG. 11. Body Twist sequence begins from Dorsal Straddle position (Fig. 10A, above) followed by: (A) Body Twist; (B) lizards break apart from force generated during Body Twist; (C) remount into Body Twist with positions switched; (D) then into another Dorsal Straddle with positions switched.

are active on a daily basis, but not for *Heloderma suspectum*.

Food storage is directly proportional to mass ($M^{1.0}$; Calder, 1984), and in squamate reptiles metabolic rate (MR) is proportional to $M^{0.80}$ (Andrews and Pough, 1985). The amount of time an animal can subsist between meals is proportional to storage/MR or $M^{0.20}$. Larger animals can thus subsist longer between meals. The relative large body size, low resting metabolic rate, and ability to take large meals make frequent foraging activity unnecessary for Gila monsters, and greatly reduces their activity costs. These traits contribute to the ability to exploit a food resource, the contents of vertebrate nests, upon which few other reptiles specialize. Three large meals, comparable in size to some taken by lizards in this study, can supply the yearly maintenance energy demands of an adult male Gila monster (Beck, 1986). Knowledge of the activity and energetics of additional large-bodied, less active species may help to refine current ideas of lizard energetics that have been formulated largely from smaller species that are active daily during their activity seasons.

Intraspecific Interactions.—From late April through late May some shelters were shared by as many as six Gila monsters concurrently in a rocky area at the north end of the study site. This area is not a "den" site where the reptiles congregate in the fall, overwinter, and emerge in the spring; rather, while some lizards may overwinter in this area, others return after overwintering about 1 km away. One large radio-equipped male, PC14, returned to this area in April 1984 after emerging from its winter shelter at the south end of the canyon, fought with another male, and then may have mated. The lizard's sequential movements and shelter locations are described below (see also Fig. 4, shelters #20-34, and Appendix 2). This lizard had foraged successfully shortly after spring emergence; his late-fall body mass of 720 g (6 Nov., 1983) had increased to 880 g after defecating 40 g of *Sylvilagus auduboni* remains on 17 April 1984. On 20 April, PC14 traveled more than 1 km to the NW (21, Fig. 4), into a shelter previously used by female PC20 in June, 1983. By 26 April, PC14 had moved another 450 m E onto a S-facing lava slope at the N end of the study site and into a shelter (23, Fig. 4) used 1 June, 1983 by PC18, another large male (shelter #6, Fig. 4). He spent most of the morning and early afternoon in the shelter, emerging periodically to bask (Fig. 3). By 1516 h his body temperature had increased to 33.6 C and he fought with an unmarked male, PC25, at the shelter entrance. Selected photographs of the fight, which lasted nearly 3 h, comprise Figs. 10 and 11.

Nine of the ten major behavioral acts recorded in a combat interaction between two captive male *Heloderma suspectum* by Demeter (1986) were exhibited by these two lizards, as follows: Dorsal Straddle (Fig. 10A); Frontal Head Nudge (Fig. 10B, C); Lateral Head Shove (Fig. 10B); Neck Arch (Fig. 10C); Tail Wrap (Fig. 10A); Lateral Head Bite; Lateral Tail Thrash; Dorsal Head Pin; and Roll.

Seven additional major behavioral acts were identified in these Gila monsters, as follows. Head Raise: raising of head and stiffening of front limbs by inferior lizard following a Neck Arch; done in response to head nudge and shove by the other lizard (Fig. 10C). Circling: moving in a semi-circular path around another lizard (Fig. 10D). Body Twist: while in Dorsal Straddle, twisting of body by the inferior lizard and placing the gular region against the neck of the superior lizard so that the bodies are entwined. The superior lizard responded with a Neck Arch (Fig. 11A). Lateral Rocking: rocking motion from side to side while in Dorsal Straddle, often resulting in a Roll. Initiated by the inferior lizard; apparently serves to remove superior lizard by forcing separation. Dorsal Body Press: turning and pressing the dorsal body surface of the superior lizard against the dorsum of the inferior lizard. Performed under boulders where the superior lizard pressed the inferior lizard downward by pushing against a boulder with the forelimbs. High Stand: standing side by side, each lizard performing head raise. Scoop: pressing the snout under another lizard, scooping it upward.

Thirteen individual "bouts" were observed. A bout refers (as in Demeter, 1986) to a repeated series of movements by the combatants between initial physical contact and separation. A typical bout lasted 10 min (range = 4-15 min) and each consisted of three distinct sequences. (1) Upon approach, lizards performed Head Nudge, Shove, Neck Arch, and Head Raise, often switching roles. (2) The aggressor mounted the other lizard in a Dorsal Straddle. The lizards repeatedly performed Tail Wrap, unwrapping tails at intervals. The inferior lizard typically responded to a Dorsal Straddle with a Neck Arch, while the superior lizard performed a Dorsal Head Pin. The superior lizard also performed a Tail Thrash in a few bouts. Sequence 2 lasted the longest of the three, and considerable struggling ensued. The inferior lizard often walked with the superior lizard clinging to his dorsum. Lateral Rocking could separate the lizards but, if not separated, they usually proceeded into a Body Twist. (3) The inferior lizard initiated a Body Twist, and the two lizards remained in that position until one gained the superior position in a Dorsal Straddle or they broke apart, sometimes from the force exerted during twisting (Fig. 11A-D). Circling sometimes preceded sequence 1 above.

The objective during each bout was apparently to gain and maintain a superior position in the Dorsal Straddle. The inferiorly-positioned lizard initiated a Lateral Roll or Body Twist apparently in an effort to break the Dorsal Straddle and gain the top position. In one bout, however, the superior lizard initiated a change of positions that immediately resulted in separation.

After 2.5 h the lizards separated and PC25 moved upslope under a lava boulder. PC14 followed and crawled around several boulders adjacent to PC25. After 15 min PC14 crawled upslope and back into the shelter he had used earlier in the day. PC25 followed PC14 into the same shelter 3 min later, at 1824 h. Later that evening PC25 left the shelter. He was next seen above ground at 1019 h the following morning, moving upslope 3 m southeast from PC14's shelter. PC25 continued upslope and was not seen again on the lava slope.

PC14 remained at the shelter throughout the following day (27 April). He emerged periodically to bask at the shelter entrance (see Fig. 3) and made one 20 min round trip downslope at 1320 h. On 28 April at 1225 h, PC14 was rubbing his cloacal area on several lava boulders and grasses approximately 5 m W of his shelter. Later in the day he moved into a new shelter (24, Fig. 4), 20 m downslope to the SW.

On 29 April, PC14 spent most of the morning basking intermittently at his shelter entrance (Fig. 3). At 1525 h another Gila monster (PC26, sex unconfirmed) crawled into the shelter with PC14. Initially considerable hissing ensued, then the two lizards positioned themselves side by side facing the shelter entrance. They remained in the shelter together the rest of the evening, at least 6.5 h, separating periodically as PC14 dug vigorously inside the shelter. PC26 left the shelter sometime after 2200 h and was not seen again. The following morning PC14 was still in the shelter. On 1 May he weighed 732 g, having lost 150 g since 17 April. He remained at the shelter until 2 May, and on the lava slope through 14 May. By 28 May PC14 had returned to the S end of the canyon (34, Fig. 4).

Male-male fights in *Heloderma suspectum* have been previously observed in captivity (Gates, 1956; Demeter, 1986; Lowe, pers. comm.) and in the field (Lowe et al., 1986), although detailed accounts of combat sequences have not been published for free-ranging animals. Gates (1956) observed two captive Gila monsters "fighting over a female, the third occupant of the cage" in June, 1955. He removed one of the fighting lizards and later observed copulation in the two remaining cagemates. Combat behavior reported by Demeter (1986) in captive *H. suspectum* was strikingly similar to the fight between free-ranging PC14 and PC25. A typical sequence in the captive lizards began with (1) Head Nudging and Shoving and Neck Arching, followed by (2) a Dorsal Straddle with an occasional Lateral Head Bite and Tail Thrash, and (3) a Roll that resulted in the animals disengaging and beginning a new sequence (Demeter, 1986). A major difference in the combat reported here was the Body Twist, which typically followed the Dorsal Straddle.

Validation of behaviors exhibited by captive reptiles from actual field observations is rare, and in this case serves to illustrate the stereotyped nature of fighting in male *H. suspectum*. Lowe et al. (1986) observed similar, stylized postures in the field, noting that fights can sometimes erupt into "vicious brawls," although such behavior is more common in captive individuals that do not have the same options for retreat as do free-ranging animals.

Elements of the combat ritual of *H. suspectum* resemble grappling postures of varanid combat (Carpenter et al., 1976; Davis et al., 1986), and arching and entwining postures of crotaline snake combat (Shaw, 1948; Lowe et al., 1986; Gillingham, 1987), but differ strikingly from aggressive behaviors (displays of posturing and head bobs, chases) observed in other lizard families (Carpenter and Ferguson, 1977; Demeter, 1986).

Combat interactions in squamate reptiles are usually interpreted to be tests of dominance. The "winner" is able to display superior physical strength, usually by forcing the subordinate to the ground until the subordinate initiates an escape response (Auffenburg, 1981; Gillingham, 1987). The winner is usually the larger animal. The resident may also have an advantage, although it can be supplanted by a larger intruder (Gillingham, 1987). The radio-implanted Gila monster (PC14) had been on the lava slope the previous year, and for three days before the fight with PC25. It was most likely the resident. Although they were fairly close in size (PC25's exact size was not recorded) PC14 (SVL 343 mm, TL 498 mm) appeared slightly larger. Carpenter et al. (1976) interpreted the winner of bouts in *Varanus gilleni* as the male in the superior position at the end of each bout sequence. Using this criterion, PC14 won 8 bouts and PC25 won 5. On two occasions during the fight, PC25 retreated and PC14 pursued, although PC25 was still willing to partake in another bout as PC14 approached. It is not possible to know with certainty which, if either, was the winner of the combat. Because he was the resident, and the perceived "winner" of the majority of the bouts, PC14 most likely "won" the fight. Moreover, PC14 remained near the shelter for several days after PC25 had left the immediate area.

The cloacal rubbing behavior of PC14 near its early May shelters on the lava slope is noteworthy. It is likely a form of chemical communication used by *H. suspectum*, possibly to aid in establishment of the social hierarchy in communal areas. *Varanus komodoensis* may communicate using scent signals associated with fecal material deposited near thermoregulatory sites and along trails (Auffenberg, 1981).

The interaction between PC14 and PC26, the Gila monster that entered PC14's shelter 3 days after the fight, is difficult to interpret fully. Only the snouts of the lizards were visible at the shelter entrance. While PC14 was not digging, they lay side by side with little movement. Their interaction was considerably less aggressive than was the combat between PC14 and PC25. No biting or struggling was observed. PC14 and PC26 may have mated in the shelter. They were oriented in a position similar to a typical *Heloderma* mating posture (Gates, 1956). This interpretation is consistent with the hypothesis that male squamate reptiles fight in order to gain access to females. Copulation after combat has been commonly observed in captive reptiles (Gates, 1956; Carpenter and Ferguson, 1977).

These behavioral observations confirm that Gila monsters have a definite social system. These seemingly solitary lizards are not roaming aimlessly when searching for potential mates or foraging sites. Common shelter use and seasonal movements that bring individuals back to communal areas, establishment of dominance through male-male combat, and scent marking are all elements of a structured social system.

During combat, lizards appeared to approach the limits of their physical endurance, especially during the Dorsal Straddle, Tail Thrash and Body Twist. Their struggles during the three-hour fight left them nearly 20 m from their starting point. Ambient temperature was low (10 C) during most of the fight; by the time they had completed the struggle, both lizards were slow in righting themselves, and PC14's body temperature had dropped from 33.6 to 17.3 C. At 1630 h, light hail was falling.

The Varanoidea (Helodermatidae and Varanidae, Pregill et al., 1986) are unique among lizards in their high capacities for sustained aerobic activity (Bennett, 1983; John-Alder et al., 1983). At 25 C, *Heloderma suspectum* can sustain aerobic activity at a higher oxygen consumption rate than any other lizard measured (John-Alder et al., 1983). It has been suggested that aerobic endurance should be best developed in active lizards that search for widely distributed prey (Pough, 1983). Although the Varanidae fit this description (Bennett, 1983), the Teidae, which includes highly active, widely foraging predators, have aerobic capacities more typical of less active iguanids (Bennett, 1983; but see Garland, 1988).

The high aerobic capacities of helodermatids probably have little to do with locomotor efficiency and foraging. In the laboratory they are able to sustain a maximum aerobic speed of 0.7–1.0 km/h within their preferred temperature range (John-Alder et al., 1983), but typically forage at one third that pace. *Heloderma* does not rely on speed as a predator escape response; unlike most lizards, it is incapable of high-speed sprints. Secretive habits, cryptic coloration, and venom are its defenses against predators (Lowe et al., 1986; Greene, 1988).

The high endurance capacity of *H. suspectum* may be a pleisiomorphy from its ancestral varanoid stock, and may play a minor role in the ecology of this species today, but there are some interesting implications when viewed in the context of the intensive male-male combat rituals. Helodermatids and varanids are unique among lizards in having combat interactions that involve intensive grapping postures that potentially test the limits of physical endurance (Murphy and Mitchell, 1974; Carpenter, et al., 1976; Davis et al., 1986; Demeter, 1986; Lowe et al., 1986). In anurans, winners of male-male fights, which often take the form of intensive "wrestling matches," enjoy higher reproductive success (Wells, 1977, 1979; Pough, 1983). Those with greater endurance may thus have higher reproductive success. If male reproductive success in helodermatids and varanids is related to success in combat, selection for physical endurance during intraspecific combat may have played a role in the evolution of high aerobic capacities in lizards.

Acknowledgments.—Many thanks to J. A. MacMahon for inspiration and guidance throughout this work, and to J. Glenn for almost two decades of encouragement and support. E. Coombs and R. Foote were instrumental in laying the foundation of much of the fieldwork. I am also grateful to E. Coombs for generously providing unpublished field records and sharing his field expertise. The encouragement of C. H. Lowe during the latter part of this work is gratefully acknowledged. Special thanks go to my parents Leia and Ted Beck. This work was part of a M.Sc. thesis at Utah State University. I thank my graduate committee members, T. Bunch, J. Gessaman, and J. A. MacMahon. For field and/or technical assistance I am grateful to A. Barnum, J. Beck, G. Childs, J. Cline, M. Coffeen, L. Edwards, C. Ernstein, L. Finchum, J. Haim, L. Krumpter, M. Mesch, G. Pascoe, R. Parmenter, Quoya, R. Rumsey, J. Wrublik, and E. Zurcher. Spearex International granted access to the study site and provided aerial photographs. Field accommodations were provided by M. Coffeen of the Utah Division of Wildlife Resources and D. Emery and G. Pascoe of Snow Canyon State Park. I thank C. M. Bogert, K. Ernest, C. H. Lowe, and D. Vleck for helpful comments on the manuscript. Financial assistance was provided by Utah State University Department of Biology and Ecology Center, Utah State Division of Wildlife Resources Nongame Section, Utah Audubon Society, and a Grant-in-Aid from Sigma Xi.

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Accepted: 30 May 1989.

Appendix 1

Body masses and lengths of *Heloderma suspectum cinctum* captured on the study site. Data provided are: lizard no., mass (g), SVL, and TL (mm). PC23, 145, 233, 348; SC1, 273, 290, 424; SC3, 451, 291, 431; PC22, 346, 300, 436; PC4, 338, 291, 446; PC21A, 265, 293, 447; PC13, 450, 306, 453; PC16B, 352, 310, 459; PC17, 350, 309, 460; PC6, 512, 331, 465; PC1,—, 314, 466; PC21B, 345, 328, 468; PC3, 462, 317, 472; PC16A, 480, 324, 476; PC19, —, 336, 477; PC11, —, 310, 478; PC9, 672, 345, 482; PC5, —, 320, 485; PC2, —, 326, 487; PC8, 555, 330, 493; SC2, 688, 339, 494; PC14, 880, 343, 498; SC5, 575; 342; 502, PC10, 610, 338, 508; PC18, 790, 343, 508; SC4, 469, 348, 513; PC20, 532, 360, 529. Mean values: mass, 479 g; SVL, 320 mm; and TL, 471 mm.

Appendix 2

Dates of sequential shelter use (day/month/yr) by Gila monsters as shown in Fig. 4. Numbers preceding dates below correspond to numbers next to shelters in Fig. 4.

PC14: 1 = 4/5/83, 2 = 5/5-9/5/83, 3a = 9/5-13/5/83, 3b = 14/5-24/5/83, 3c = 25/5/83, 4 = 26/5/83, 5 = 27/5/83, 6 = 28/5-8/6/83, 7 = 10/6-15/6/83, 8a = 16/6-28/6/83, 8b = 29/6-7/7/83, 9 = 8/7/83, 10 = 10/7/83, 11 = 14/7-27/7/83, 12 = 21/8-7/9/83, 13 = 8/9-9/9/83, 14 = 10/9-8/10/83, 15 = 9/10-23/10/83, 16 = 30/10/83, 17 = 31/12/83, 18 = 18/2-29/3/84, 19 = 13/4-16/4/84, 20 = 17/4-19/4/84, 21 = 20/4-23/4/84, 22 = 23/4-24/4/84, 23 = 26/4-28/4/84, 24 = 28/4-2/5/84, 25 = 2/5-4/5/84, 26 = 12/5-14/5/84, 27 = 14/5/84, 28 = 15/5-16/5/84, 29 = 17/5/84, 30 = 18/5-20/5/84, 31 = 21/5/84, 32 = 22/5-24/5/84, 33 = 25/5-27/5/84, 34 = 28/5-30/5/84, 35 = 31/5-2/6/84, 36 = 3/6-6/6/84, 37 = 7/6-9/6/84, 38 = 10/6/84, 39 = 11/6/84.

PC18: 1 = 13/5/83, 2 = 24/5/83, 3 = 26/5/83, 4 = 27/5-30/5/83, 5 = 31/5/83, 6 = 1/6/83, 7 = 2/6/83, 8 = 3/6-4/6/83, 9 = 5/6/83, 10 = 6/6/83, 11 = 16/6/83, 12 = 19/6/83, 13 = 23/6/83, 14 = 24/6-26/6/83, 15 = 27/6/83, 16 = 29/6/83, 17 = 1/7-3/7/83, 18 = 14/7-20/7/83, 19 = 27/7-30/9/83, 20 = 2/10/83, 21 = 8/10/83, 22 = 16/10-6/11/83, 23 = 30/12/83-18/2/84.

PC20: 1 = 16/5/83, 2 = 24/5/83, 3 = 24/5-27/5/83, 4 = 28/5-9/6/83, 5 = 10/6-18/6/83, 6 = 19/6-23/6/83, 7 = 24/6-28/6/83, 8 = 29/6/83, 9 = 8/7-25/7/83, 10 = 27/7/83, 11 = 20/8-21/9/83, 12 = 21/9-28/9/83, 13 = 28/9/83, 14 = 6/11/83, 15 = 31/12/83-13/4/84.

THE EFFECTS OF WILDFIRE ON REPTILE POPULATIONS IN THE MOJAVE NATIONAL PRESERVE, CALIFORNIA

Final Report
January 2009

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ACKNOWLEDGEMENTS

I cannot express enough appreciation for the generous funding provided by the California Desert Research Fund at the Community Foundation, the California Desert Studies Consortium, and California State University. Also, to the Desert Studies Center at Zzyzx, for use of equipment and facilities.

I would also like to thank the individuals at the Mojave National Preserve who made this research possible, particularly David Nichols and Debra Hughson. Also, my advisor Dr. James W. Archie who introduced me to the study area and supported my research decisions. My sincere gratitude goes to Dr. Dessie Underwood, Dr. Esteban Fernandez-Juricic, Dr. Simon Malcomber, Dr. Lynn Zimmerman, Terry Christopher, and Alicia Fox for assistance with experimental design and proofreading.

I am grateful to Marcello Aguirre, Matt Baxter, James Dutcher, Robert Dutcher, Cristina Francois, Erin Guinn, Ashley Jones, Stephen Jones, Sara Louwsma, Jeff Putzi, Jim Toenjis, and members of the California Conservation Core for field assistance and willingness to work long hours on this project.

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ABSTRACT

During the summer of 2005, lightning caused wildfires in the Mojave National Preserve, California. The fires burned 287 km^2 and left unburned patches surrounded by burned vegetation.

This study examined the effects of the wildfires on reptile diversity and *Uta stansburiana* (side-blotched lizard) abundance by conducting transect surveys at patches and along the fire perimeter in burned and unburned habitats. Temperature and vegetation cover data were recorded at each site. Pitfall trapping was conducted at patch sites to monitor *U. stansburiana* movements.

The wildfires resulted in higher temperatures in burned areas and more cover in unburned areas. Burned and unburned habitats had comparable reptile diversity and *U. stansburiana* was most abundant. *U. stansburiana* in unburned perimeter locations were constant, indicating this population was the least impacted. In 2006 the most were found along the burned side of the perimeter where high temperatures may have allowed for optimal basking sites. In 2007 the temperatures increased and the individuals in this area decreased by half.

The number of individuals moving out of patches was consistent but the number moving in increased, indicating a preference for unburned areas. The low numbers recorded in this study suggest that the wildfire negatively impacted the herpetological community.

INTRODUCTION

Ecological Role of Wildfire

Disturbance is common to all ecosystems and results in altered landscapes that differ from original habitat in floral and faunal composition and abundance (Reice, 2001). Natural disturbance, particularly wildfire, causes habitat changes by killing mature plants, seedlings, and seeds. Fire also alters the nutrient levels and water absorption abilities of soil. The effects of fire result in changes in microclimate, particularly post-fire soil temperature and moisture, and drastically reduce ground cover (Brooks, 2002; Odion and Davies, 2000).

In systems that are fire adapted this disturbance is essential for floral and faunal persistence (Parr and Chown, 2003). However, in areas that have not historically been subjected to frequent or intensive fire regimes, such as arid ecosystems, species diversity and abundance suffer due to mortality during the fire and the subsequent alteration of habitat (Brooks and Matchett, 2003; Taylor and Fox, 2001).

The unpredictable nature of wildfires often creates a habitat framework of small unburned patches within what was once contiguous habitat (Parr and Chown, 2003; Turner et al., 1997). Wildfire thus fragments habitat by creating small patches that are separated from one another by a habitat type that no longer resembles original conditions. Fragmentation due to wildfire does not necessarily indicate permanent habitat loss (Fahrig, 2003). The effects of wildfire are unpredictable and recovery is highly variable depending on location, burn severity, intensity, and post-fire plant succession (Davies et al., 2001; McKenzie et al., 2004; Reice, 2001; Turner et al., 1997).

Fragmentation, Wildfire, and Reptile Communities

A review of herpetofaunal response to fire found that many animals exhibit panic and experience high rates of mortality (Russell et al., 1999). Because of the need for thermoregulatory, foraging, and protected sites, reptiles are highly dependent on habitat structure and fire has been shown to reduce their abundance and limit movements (Setser and Cavitt, 2003; Valentine et al., 2007). However, unburned habitat patches may serve as refugia for reptile populations that survive in the patch, nearby rock outcroppings, or burrows in the ground (Faria et al., 2004; Friend, 1993).

While vegetated areas produce shaded microclimates where soil temperatures are less extreme and moisture is preserved, disturbed habitats generally show reduced vegetation complexity (Patten and Smith, 1975). Habitats dominated by invasive plants also show decreased numbers of invertebrates. This reduction in thermoregulatory and food resources results in a decrease in total reptile abundance. Studies in disturbed areas in southern California, Australia, and Egypt have indicated that reptile abundance and diversity were positively correlated with vegetation percent cover and native vegetation (Attum et al., 2006; Russell et al., 1999; Valentine et al., 2007).

Wildfire and Exotic Plants in Desert Regions

Historically, large wildfires in desert communities have been uncommon because without a relatively large, continuous fuel source, wildfires tend to have reduced size and intensity (Hanes, 1971; Reice, 2001). However, in North American deserts, wildfires have become increasingly frequent since the 1970s. This is because of the introduction of exotic plant species, particularly *Erodium cicutarium* (fillaree), *Bromus sp.* (foxtail, cheatgrass) and *Schismus sp.* (Mediterranean grass). These species, native to Europe, Africa, and Asia, are adapted to fire regimes in arid ecosystems and create a blanket of dry vegetation that facilitates the spread of wildfire by creating a layer of dry, fast burning fuel. Recurrent fire in the American southwest amplifies the presence of these alien species, which have been shown to replace long-lived natives, changing the floral composition (Brooks, 1999, 2000a, 2000b; Brooks and Matchett, 2003; Esque, 1999; Young, 2000). Because of these effects wildfire is currently considered one of the main threats to native species in the Mojave (Brooks, 2002).

Wildfire in the Mojave Desert

The Mojave Desert is subjected to frequent lightning strikes during the summer monsoon season (May-August) and wildfires are generally caused by dry lightning storms during this period (Esque et al., 2003). Large fires are infrequent events in areas with native vegetation. Consequently, wildfires in the Mojave have not been well studied, and their effects have yet to be well documented (National Park Service, 2003).

On 22 June 2005, a series of dry seasonal storms passed through the Mojave National Preserve (MNP), San Bernardino County, California. Dry lightning caused multiple fires that merged to become the Hackberry complex of wildfires. The fires burned for seven days and were contained on 28 June 2005. A total of 287 km^2 burned within the Preserve between elevations of 1097-2012 m (http://www.nps.gov/moja/parkmgmt/upload/Hackberry_BAER_Plan%2006-05.pdf). Within the Hackberry region the dominant form of vegetation affected by the fires was juniper woodland (Mojave National Preserve Maps, 2005). However, the fire did not consume all of the vegetation and the burned landscape contained several patches of unburned habitat. These habitat islands were surrounded on all sides by burned vegetation resulting in a fragmentation of the habitat.

Objectives

The Mojave is home to an incredible array of reptiles and the Hackberry region supported many species. The objective of this study was to determine the effects of the Hackberry wildfires on the herpetofaunal community. Based on previous research, most of which indicates increased mortality as well as limited habitat utilization and movement following a wildfire, it was reasonable to expect populations in the Mojave would show similar responses. I expected to find increased ground and subterranean temperatures and decreased vegetation cover in burned areas, with cover increasing through time, but not achieving pre-burn proportions or composition. The burned locations were expected to support fewer reptile species based on the resources available. As density increased with time, more individuals were expected to disperse from unburned habitat patch locations. I tested the hypothesis that movement into and out of unburned habitat patches by would change with time. I predicted that in the first year of this study more individuals would migrate into unburned habitat patches and that in the second year the individuals would disperse out of patches as lizard density and vegetation in burned areas increased.

MATERIALS AND METHODS

Site Selection

The Mojave National Preserve (MNP) lies in the eastern portion of the Mojave Desert of California. The Preserve is located to the south of Death Valley and north of Joshua Tree National Parks, between Interstates 15 and 40. The infrequency of large wildfires, remoteness of the area, and limited impact from development make the MNP an excellent area to study. Permits were obtained from the National Park Service, California Department of Fish and Game, and California State University (IACUC number 279).

Sampling for this study was concentrated in what was predominantly juniper woodland between the elevations of 1,370 m-1,675 m (Mojave National Preserve Maps, 2005). Sites were located near Cedar Canyon and Black Canyon roads, in the Mid-Hills area (Figure 1). Seven unburned habitat patches, that were surrounded by burned landscape on all sides, and seven perimeter locations along the fire edge were surveyed. Patch sites were mapped using a handheld Global Positioning System (GPS) unit and ranged in size from approximately 1,527-36,580 m^2.

Temperature Data Collection

Ambient, ground, and subterranean temperatures were collected using a handheld Ashcroft dial thermometer. All temperatures were recorded after the thermometer was placed in a temporarily shaded area for 2 minutes and collected at the start of each transect survey on both the burned and unburned sides. Air temperature was recorded after holding the thermometer several feet above the ground, ground temperature was recorded after placing the thermometer on the soil surface, and subterranean temperature was recorded after placing the tip of the thermometer 3-5 cm into the soil.

At one habitat patch an Eastman maximum/minimum thermometer was installed on a wooden stake 50 cm above the ground to determine air temperature extremes.

Transect Design

Transects were used to assess species diversity and abundance across distinct habitat types with clearly defined borders (Morris, 1995). At each sampling site three parallel transects that crossed the transition zone from burned into unburned habitat were monitored. Each transect was a straight-line 50 m in length, and bisected the habitat, with 25 m in each habitat type. Transects were separated from replicates by 20 m (Figure 2). Transects were measured out using a 25 m Lufkin tape measure. I used GPS waypoints to mark the start and end locations of each transect (Table 1).

Vegetation Point-Intercept Transect Surveys

Vegetation point-intercept transects were conducted by walking the transect lines described above and recording vegetation height every five meters. At each point a 7-cm diameter pole was placed directly on the point and the height of each plant that touched recorded (Barbour et al., 1999). Plant height was classified as <10 cm, 10-30 cm, 30-50 cm, 50 cm-1 m, and >1 m. Dead or severely burned vegetation was not recorded. I recorded vegetation once a month from May-October 2006 and March-August 2007. A total of 504 vegetation transects were conducted (14 sites x 3 replicates x 12 times).

Reptile Transect Surveys

During the fall and spring, transect surveys were conducted throughout the day; however, in the summer, when temperatures were at their highest, transect surveys were conducted in the morning and late afternoon. In order to find lizards by direct observation in both burned and unburned areas, each transect line was walked two times and a snake stick used to flush lizards from grasses and shrubs. Sighting effort was concentrated to 5 m on either side of the transect line. Reptile species were identified, and distance along the transect line was documented in 5 m segments. During the course of this study I conducted a total of 1,542 transects (14 sites x 3 replicates x 36 times).

Pitfall Trapping

Pitfall arrays were established at the seven habitat patches to determine the diversity of reptile species in patches and monitor movements (Table 2). At each patch six 5-gallon plastic buckets were buried so the rims were flush with the soil surface. Three drainage holes were drilled into the bottom of all traps to prevent the accumulation of water. Each trap was fitted with a cover to provide shade and protection. The covers were inverted plastic bucket lids with three 5 by 5 cm tall pieces of wood attached at equal distances along the edge (Fisher et al., 2004). Attached to each cover was a 50 cm long piece of jute that served as a rodent escape string to minimize mortality. The pitfall traps were stocked with two to three small pieces of kibble, a 12 cm long by 5 cm diameter PVC pipe piece lined with small amounts of batting, and a 3-5 cm piece of wet sponge to keep trapped animals hydrated (Karraker, 2001; Persons and Nowak, 2006). When the wet sponge attracted ants it was temporarily removed (Fisher et al., 2004). When in use, traps were checked every 12 hours. When not in use, the bucket lid was securely fastened, rocks placed on the lid, and soil placed loosely over the lid to seal the trap.

Each bucket trap was separated by 7.5 m of 30 cm tall tan cloth drift fencing, which guided reptiles differentially into traps from burned and unburned habitats. Each array was arranged in a zigzag pattern, providing more intercept angles (Fisher et al., 2004). The buckets were completely fenced on three sides, with three buckets fenced on the patch side and three buckets fenced on the burn side (Figure 3). This design allowed for the study of directional movement, as individuals captured in buckets fenced on the patch side came from the burn area and individuals captured in buckets fenced on the burn side were moving away from the patch. The fencing was held in place by wooden stakes and buried 7-12 cm into the ground.

The array and trap numbers of all captured lizards were recorded. A small tissue sample was taken from the tail tip and preserved in 95% ethanol for possible later genetic analysis (Hirsch et al., 2002). For easy recognition of an individual from a distance captured lizards were marked, based on their site location, with nail polish. Because they were captured in higher numbers, *Uta stansburiana* (side-blotched lizard) were also marked by toe clipping one digit (Ferner, 1979; Swingland, 1978). Small mammals (that did not escape via the escape string) and captured invertebrates were recorded to species and family, respectively. No mortalities occurred during the course of this study and all individuals were released at the site of capture.

Trapping was conducted on a monthly basis, between temperatures of 2-42°C. Traps were closed during heavy rains and when temperatures reached 0°C to prevent mortality. Trap effort for this study was defined as the number of open traps per trap session, with a session being 12 hours. Trap effort was 5,324 trap days/nights (7 arrays x 6 buckets in each array x 135 trap sessions-346 trap closures due to unforeseen circumstances).

Statistical Analysis

A Shapiro-Wilk test for normality was conducted, and when data were not normally distributed transformations using log(x), ln(x), x^2, and $\sqrt{x}$ were performed. Analyses involving herpetological community structure were conducted using PRIMER. All other analyses were completed using PRISM statistical software.

The mean, standard deviation, and minimum/maximum temperatures were calculated for temperature data. Air and ground surface temperatures in warm (May-August 2006 and 2007) and cold seasons (September-October 2006 and March-April 2007) were analyzed using paired *t*-tests.

Vegetation data were analyzed using χ^2, with the means and standard deviations of each plant height class calculated to compare plant heights in burned and unburned areas.

The observation rate of reptile species seen during transect surveys was calculated. ANOSIM (analysis of similarity) of species diversity between years and in burned and vegetated habitats and SIMPER (similarity percentages) analyses were conducted (Clarke, 1993). Transect data collected on *U. stansburiana* locations by line segment through time in each habitat type were analyzed using Friedman randomized block test, χ^2, and Fisher's Exact tests.

The capture rate of each lizard species caught during pitfall trapping was calculated along with the recapture rate for *U. stansburiana*. ANOSIM and SIMPER analyses were conducted to determine dominance in the herpetological community. Abundance data collected on trapped *U. stansburiana* were analyzed with a paired *t*-test and a Fisher's Exact test. Species of mammal and family of invertebrate captured were also tallied.

RESULTS

Ambient Air, Ground Surface, and Subterranean Temperatures

The mean ambient air temperature (±*SD*) for the 2006 and 2007 warm seasons combined was 31.1 ± 5.0ºC and for cold seasons was 20.6 ± 7.2ºC. Ambient air temperatures in the warm season of 2007 were significantly higher than 2006 ($t = 5.420$, $df = 195$, $p < 0.0001$, $\bar{x}$ 2006 = 29.6 ± 5.1, $\bar{x}$ 2007 = 32.4 ± 4.5). The means of the cold seasons were not significantly different ($t = 0.3196$, $df = 55$, $p = 0.7505$, $\bar{x} = 20.6 \pm 7.2$) from one another (Figure 4a).

Ground surface temperature data for 2006 and 2007 were divided by habitat type, season, and year creating data sets for 2006 and 2007 of warm season unburned, warm season burned, cold season unburned, and cold season burned. Unburned habitats were not found to be significantly different between years in the warm season ($t = 0.0206$, $df = 194$, $p = 0.9836$, $\bar{x} = 31.5 \pm 5.9$). Significant differences were found in the cold season ($t = 3.570$, $df = 55$, $p = 0.0007$, $\bar{x}$ 2006 = 19.3 ± 5.2, $\bar{x}$ 2007 = 16.7 ± 6.9), with 2006 being warmer. In burned habitat significant differences were not found between years in the warm season ($t = 1.091$, $df = 193$, $p = 0.2767$, $\bar{x} = 32.5 \pm 6.1$), while the 2006 cold season showed a significant difference in means between years ($t = 8.877$, $df = 52$, $p < 0.0001$, $\bar{x}$ 2006 = 19.5 ± 5.6, $\bar{x}$ 2007 = 17.5 ± 7.0). Also, burned habitats in the warm season had significantly higher temperatures ($t = 11.61$, $df = 415$, $p < 0.0001$, $\bar{x}$ unburned = 31.5 ± 5.9, $\bar{x}$ burned = 32.5 ± 6.0) than unburned. The cold season ($t = 0.6167$, $df = 112$, $p = 0.5387$, $\bar{x} = 18.2 \pm 6.3$) did not have significantly higher temperatures in burned habitats (Figure 4b).

Subterranean temperatures in the warm season of 2007 were significantly higher in both habitat types (unburned $t = 2.003$, $df = 195$, $p = 0.0466$, $\bar{x}$ 2006 = 30.6 ± 8.2, $\bar{x}$ 2007 = 31.2 ± 5.6, and burned $t = 2.239$, $df = 195$, $p = 0.0263$, $\bar{x}$ 2006 = 32.4 ± 8.3, $\bar{x} = 32.8 \pm 5.4$). I found that 2006 was significantly colder in the cold seasons in both habitats (unburned $t = 10.61$, $df = 55$, $p<0.0001$, $\bar{x}$ 2006 = 15.2 ± 4.5, $\bar{x}$ 2007 = 11.9 ± 6.4, and burned $t = 9.739$, $df = 55$, $p < 0.0001$, $\bar{x}$ 2006 = 15.7 ± 4.1, $\bar{x}$ 2007 = 12.6 ± 6.2). In the warm season subterranean temperatures in the burned area were significantly higher than in the unburned area ($t = 50.08$, $df = 417$, $p < 0.0001$, $\bar{x}$ unburned = 30.9 ± 6.9, $\bar{x}$ burned = 32.6 ± 6.9). Subterranean temperatures in burned habitats were also higher in the cold season ($t = 7.641$, $df = 111$, $p < 0.0001$, $\bar{x}$ unburned = 13.5 ± 5.5, $\bar{x}$ burned = 14.2 ± 5.1) during this study (Figure 4c).

During pitfall trapping the minimum air temperature recorded was 0ºC and the maximum temperature was 42ºC.

Vegetation Point-Intercept Transect Surveys

I found that only counts of plants <10 cm tall at one site in the burned area along the fire perimeter and one site in the burned area around a habitat patch, were normally distributed. The total number of plants in the unburned areas (1,440; 68.58% total cover) was higher than in burned areas (846; 40.28% total cover). There were differences in the distribution of vegetation heights in each habitat ($\chi^2 = 389.9$, $df = 1$, $p < 0.0001$). There were significantly more plants in the burned area under 10 cm than in any other height class in either habitat (Table 3). The number of plants in burned areas in this height class increased from 2006-2007 (264 and 345 total plants). For all heights, except <10 cm, unburned habitats had more plants per site than burned. Although all plants seen were not recorded to species, of those recorded 2% and 21% were noted as *Erodium cicutarium* or a grass species in unburned areas. In burned areas this trend was reversed with *E. cicutarium* accounting for 31% and grasses making up only 7%.

Reptile Transect Surveys

During transect surveys five lizard and one snake species were observed (Table 4). Multi dimensional scaling (MDS) showed that transect sites clustered together by habitat type with the exception of two sites; one unburned patch and one burned perimeter transect location. These two sites were removed from the analysis because they had significantly more zero values and were outliers that made it impossible to determine how locations clustered. I found no significant differences in the species assemblages between years (ANOSIM, $R = 0.018$, $p = 0.271$ and $R = -0.043$, $p = 0.888$) or between unburned and burned habitats ($R = 0.053$, $p = 0.109$ and $R = 0.010$, $p = 0.333$) along the perimeter and in the patch locations, respectively. Therefore, data from 2006 and 2007 were combined and reanalyzed using ANOSIM. Species found at perimeter and patch sites did not differ significantly ($R = 0.038$, $p = 0.272$); however, differences were found ($R = 0.220$, $p = 0.022$) between unburned and burned locations. A SIMPER analysis showed that in the unburned areas, *U. stansburiana* accounted for 88.0% of individuals, with *A. tigris* and *S. occidentalis* making up 14.7% and 13.5% of individuals, respectively. In the burned areas *U. stansburiana* comprised 98.6% of individuals.

U. stansburiana abundance data were not normally distributed and a normalizing transformation could not be found. A Friedman randomized block test found no significant differences in the number of individuals seen by segment location along transects in each habitat type through time (Friedman statistic = 6.500, $p = 0.0897$). Differences were found between habitat types ($\chi^2 = 9.952$, $df = 3$, $p = 0.0190$). Burned areas around patches in 2006 and outside the perimeter in 2007 had the fewest individuals. Most *U. stansburiana* were recorded in burned areas along perimeter sites in 2006, followed by unburned patch sites in 2007 (Figure 5). Although combining perimeter and patch sites yielded more individuals found in unburned habitat ($n = 77$ compared to $n = 62$), there were no significant differences in the number of *U. stansburiana* in unburned and burned habitats (Fisher's Exact test; $p = 0.0624$). Also, no detectable differences were found when year data were combined (Fisher's Exact test; $p = 0.1201$), although burned patches had the fewest ($n = 22$), while burned perimeter and unburned patch habitats had the most individuals (both had $n = 39$). Surprisingly, significant differences were found when unburned and burned sites along the perimeter and at patch locations were combined (Fisher's Exact test; $p = 0.0258$).

Pitfall Trapping

During pitfall trapping six lizard species were captured (Table 5). MDS showed that pitfall trap sites clustered together by year with the exception of one site in a patch location in 2006, which had more zero data points than other sites. This site was removed in order to see patterns in the remaining data. Species abundance did differ significantly between years (ANOSIM, $R = 0.216$, $p = 0.044$). More individuals were captured in 2007 ($n = 60$) than 2006 ($n = 36$). Also, 2006 had one single species not captured in 2007, while 2007 had two that were not present in 2006. *U. stansburiana* dominated the herpetofaunal assemblages in both years; however, this species was represented in a higher percentage in the 2007 (SIMPER, 2006 = 92.6% and 2007 = 98.2%).

Of the 80 *U. stansburiana* captured over the course of this study, 19 were recaptures, resulting in a recapture rate of 23.75%. In 2006 there were very few recaptures (10.71%); however, 2007 saw an increase in recaptured individuals (30.77%). Recaptures of individuals were removed from statistical analyses. The total number of *U. stansburiana* captured by site were normally distributed in both years (2006 $p = 0.2601$ and 2007 $p = 0.7222$). No significant differences in the number of individuals caught between years ($t = 1.135$, $df = 12$, $p = 0.2787$) was found. No significant differences in the direction of movement of individuals was found when these data were combined for analysis (Fisher's Exact test; $df = 4$, $p = 0.2968$), even though the number of *U. stansburiana* moving into patches actually doubled (9 to 18) from 2006-2007 (Figure 6). During trapping more juveniles were captured (66%) than adults (34%), with most *U. stansburiana* being captured in 2007.

I also recorded the numbers of mammals and invertebrates captured in pitfall traps. As these individuals could easily climb the drift fencing their direction of movement could not be determined. Interestingly, the number of mammalian species captured decreased, as did the total number of individuals captured from the first to the second year (Table 6). Conversely, the number of invertebrate families and the total number of individuals captured increased from 2006-2007 (Table 7).

DISCUSSION

Temperature and Vegetation

Due to air temperature variation, 2007 was warmer than 2006, but both ground surface and subterranean temperatures were higher in burned areas than in unburned areas in both years.

The plant community in unburned areas had almost 30% more cover than burned areas and remained relatively stable through time. However, the burned areas had more than twice the number of plants in the <10 cm height class, and very few grew to over 10 cm during the course of this study. This indicates that most were low growing ground cover species. This is consistent with long term studies of plant communities in the Southwest that have found areas affected by wildfire are rapidly colonized by low growing ground cover species that are predominantly alien (Brooks, 2002; Brooks and Matchett, 2003). Additionally, soil nutrient research in the Mojave found that grasses were better competitors and often become dominant following disturbance (Brooks, 1999).

Comparison of Transect and Pitfall Data

Transect and pitfall surveys had comparable species diversity with each other. *Uta stansburiana* was the dominant species in all locations. I found the highest number along the fire perimeter on the burned side in 2006, which is similar to a study conducted after a wildfire in Arizona that found reptiles exhibited a preference for disturbed sites (Cunningham et al., 2002). However, in 2007 the number of individuals found in this area decreased by more than half. It may be that individuals utilized this area more heavily initially because the higher ground temperatures allowed for optimal basking sites. In 2007 temperatures may have become too high creating a less than ideal habitat type that did not provide a thermoregulatory gradient or enough cover (Wilson, 1991). The number of *U. stansburiana* in unburned perimeter locations was relatively constant through time, indicating that this population was the most stable. The numbers found at patches increased in burned and unburned areas, with unburned sites having more individuals.

The directional design of the pitfall arrays allowed me to assess whether individuals were moving into or out of habitat patches. However, no directional pattern was detected, likely because of the low numbers of individuals captured. However, in 2006 the number of *U. stansburiana* captured in pitfall traps at patch sites (n = 28) was comparable to the number seen during transect surveys at the same locations (n = 25). In 2007 more were captured (n = 52) than seen (n = 37). It may be that the increased temperatures in 2007 altered the movements of *U. stansburiana*, decreasing their daily activity.

Future Research Recommendations

This research would have benefited from a longer study period. Two years is not a sufficient amount of time to accurately determine trends in a fragmented system that is undergoing post-wildfire successional stages. Many environmental parameters, including yearly temperature and rainfall fluctuations, could account for the trends seen and result in notable year-to-year variability (Hirsch et al., 2002).

Conservation Implications

Although the results of a study conducted in a single location and affected by a single event may not be fully extrapolated to other locations or events, it is clear that wildfire is a serious threat to biodiversity in the Mojave. The effects of large desert fires are poorly understood, largely because this is a relatively new problem (Brooks, 2002; Brooks and Matchett, 2003). Information on floral community succession and faunal survival is useful to help understand the long-term consequences of altering landscapes, and could lead to increased control of invasive species. These species have created a positive feedback system, or a grass-fire cycle, in the Mojave. The resulting habitats are increasingly homogeneous, and provide few resources (Esque, 1999; Esque et al., 2003; Valentine et al., 2007).

The presence of *U. stansburiana* is a good indicator of the possible establishment of healthy populations of many other species. *U. stansburiana* is an abundant and widespread lizard that is a food source for many species that cannot reoccupy an area until suitable numbers of prey are present (Stebbins, 2003). Low numbers will negatively impact the community, decreasing both diversity and abundance. This study suggests that wildfire in the Mojave negatively affects the reptile community.

Due to the hostile conditions and already limited resources, desert environments are not able to maintain dense populations of wildlife, creating fragile systems composed of highly specialized species. Deserts, although coming under increasing pressure from human expansion and activities, are some of the most inhospitable and therefore remote and unexploited areas in the continental United States. Wildlands are becoming increasingly rare worldwide and few ecosystems contain organisms with such unique adaptations to extreme conditions as desert regions, making conservation in these areas a critical concern.

TABLE 1. Transect Locationss in the Hackberry Region, Mojave National Preserve

Site	Starting Easting	Starting Northing	Ending Easting	Ending Northing	Elevation (m)
Patch 1	645412	3892561	645405	3892517	1596
	645409	3892565	645438	3892531	
	645431	3892589	645438	3892543	
Patch 2	645425	3892203	645476	3892204	1591
	645422	3892195	645470	3892178	
	645438	3892181	645467	3892157	
Patch 3	642829	3887189	642812	3887237	1661
	642821	3887185	642789	3887221	
	642806	3887173	642777	3887208	
Patch 4	642810	3887316	642814	3887365	1665
	642786	3887307	642798	3887350	
	642754	3887298	642787	3887342	
Patch 5	642814	3887533	642841	3887575	1670
	642788	3887525	642821	3887566	
	642708	3887531	642806	3887571	
Patch 6	645913	3887650	642933	3887695	1684
	642929	3887649	642944	3887699	
	642954	3887662	642962	3887709	
Patch 7	643023	3887958	643039	3887909	1679
	643050	3887969	643049	3887917	
	643077	3887972	643063	3887927	
Perimeter 1	646600	3892811	646555	3892819	1594
	646598	3892786	646549	3892794	
	646586	3892763	646540	3892786	
Perimeter 2	646545	3892659	646493	3892658	1604
	646552	3892636	646500	3892638	
	646536	3892610	646488	3892620	
Perimeter 3	646524	3892565	646480	3892567	1656
	646522	3892553	646480	3892546	
	646538	3892529	646492	3892526	
Perimeter 4	646513	3892468	646465	3892474	1660
	646506	389245	646457	3892448	
	646498	3892431	646458	3892678	
Perimeter 5	646586	3892634	646587	3892681	1580
	646595	3892616	646611	3892668	
	646623	3892625	646623	3892678	
Perimeter 6	645283	3892595	645259	3893556	1582
	645262	3892604	645247	3893560	
	645244	3892615	645237	3893568	
Perimeter 7	645167	3893604	645186	3893568	1580
	645153	3893610	645175	3893571	
	645132	3893600	645150	3893554	

Note: All locations in map datum NAD83, UTM zone 11.

TABLE 2. Locations of Pitfall Trap Arrays in the Hackberry Region of the Mojave National Preserve

Array	Easting	Northing	Elevation (m)
1	645395	3892528	1596
2	645456	3892203	1591
3	642811	3887222	1661
4	642804	3887343	1665
5	642873	3887558	1670
6	642942	3887683	1684
7	643035	3887924	1679

Note: All locations in map datum NAD83, UTM zone 11.

TABLE 3. Percent Vegetation Cover in Unburned and Burned habitats by Height Class

Height Class (cm)	Unburned		Burned	
	Number	Percent Cover	Number	Percent Cover
<10	220	10.48	631	30.05
10-30	295	14.05	133	6.33
30-50	248	11.81	63	3.00
50-100	345	16.43	16	0.76
>100	332	15.81	3	0.14
Total	1440	68.58	846	40.28

TABLE 4. Reptile Species Observed During Transect Surveys

Species	2006		2007		Unburned		Burned	
	Number	Rate	Number	Rate	Number	Rate	Number	Rate
Aspidocelus tigris Western whiptail	7	0.3684	4	0.2105	11	0.2895	0	0
Gambelia wislizenii Long-nosed leopard lizard	2	0.1053	0	0	1	0.0263	1	0.0263
Masticophis taeniatus Striped whipsnake	1	0.0526	0	0	0	0	1	0.0263
Phrynosoma platyrhinos Desert horned lizard	0	0	1	0.0526	0	0	1	0.0263
Sceloporus occidentalis Western fence lizard	8	0.4211	7	0.3684	5	0.1316	10	0.2632
Uta stansburiana Side-blotched lizard	80	4.2105	56	2.9474	75	1.9737	61	1.6053
Total	98	5.1579	68	3.5789	92	2.4211	74	1.7105

Note: Observation rates were calculated using number of observations/number of transects conducted (Persons and Nowak, 2006).

TABLE 5. Reptile Species Captured During Pitfall Trapping

Species	2006		2007	
	Number	Capture Rate	Number	Capture Rate
Aspidocelus tigris Western whiptail	5	0.0725	1	0.0145
Gambelia wislizenii Long-nosed leopard lizard	1	0.0145	0	0
Sceloporus magister Desert spiny lizard	0	0	3	0.0435
Sceloporus occidentalis Western fence lizard	2	0.0290	5	0.0435
Uta stansburiana Side-blotched lizard	28	0.4056	52	0.7536
Xantusia vigilis Desert night lizard	0	0	1	0.0145
Total	36	0.5216	62	0.8969

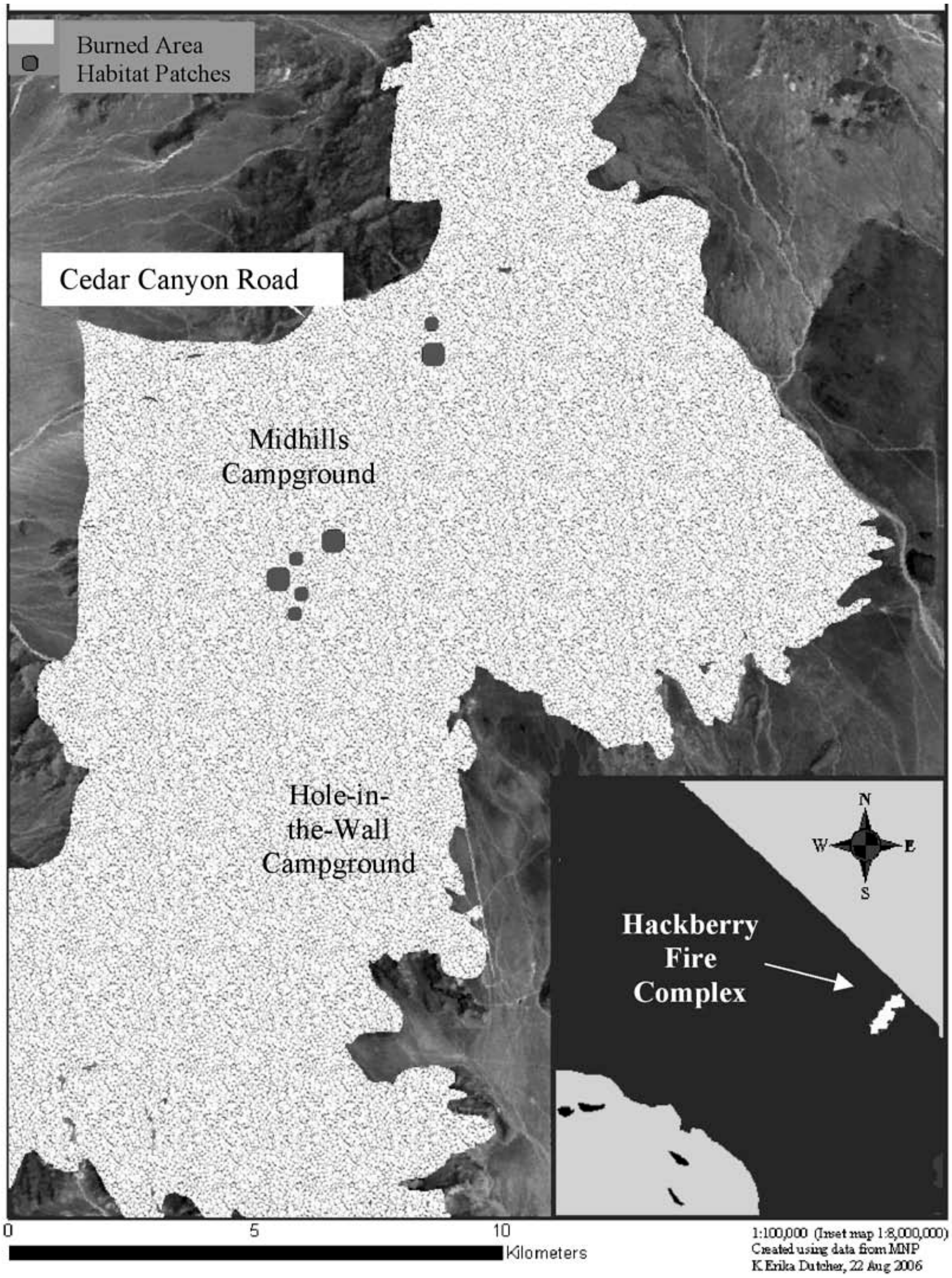
Note: Capture rates were calculated using number of captures/number of pitfall trap sessions conducted (Persons and Nowak, 2006).

TABLE 6. Mammal Species Captured During Pitfall Trapping

Species	2006	2007
Dipodomys deserti Desert kangaroo rat	6	3
Lagurus curtatus Sagebrush vole	3	0
Perognathus longimembris Little pocket mouse	1	1
Perognathus penicillatus Desert pocket mouse	0	1
Peromyscus sp. Pygmy mouse species	3	0
Thomomys bottae Valley pocket gopher	1	1
Total Number of Individuals	14	6
Total Number of Species	5	4

TABLE 7. Invertebrate Families Captured During Pitfall Trapping

Family	2006	2007
Caraboctonidae (Desert scorpions)	35	71
Cerambycidae (Long-horned beetles)	0	1
Cicadidae (Cicadas)	0	1
Eremobatidae (Windscorpions)	31	35
Gryllacrididae (Camel crickets)	98	152
Gryllidae (Crickets)	3	0
Mantidae (Mantids)	1	1
Mutillidae (Velvet ants)	0	2
Myrmeleontidae (Antlions)	0	1
Pompilidae (Tarantula hawks)	0	1
Reduviidae (Assassin bugs)	0	13
Scolopendridae (Multicolored centipedes)	2	0
Tenebrionidae (Darkling beetles)	483	623
Theraphosidae (Blonde tarantulas)	0	1
Total Number of Individuals	653	902
Total Number of Families	7	12



1:100,000 (Inset map 1:8,000,000)
Created using data from MNP
K Erika Dutcher, 22 Aug 2006

FIGURE 1. Habitat patch locations within the Hackberry region of the Mojave National Preserve. Habitat patch size not to scale. The subset map shows the location of the Hackberry wildfire in Southern California. Map created by K. Erika Dutcher and Dr. D. Underwood using data from the National Park Service, 2006.

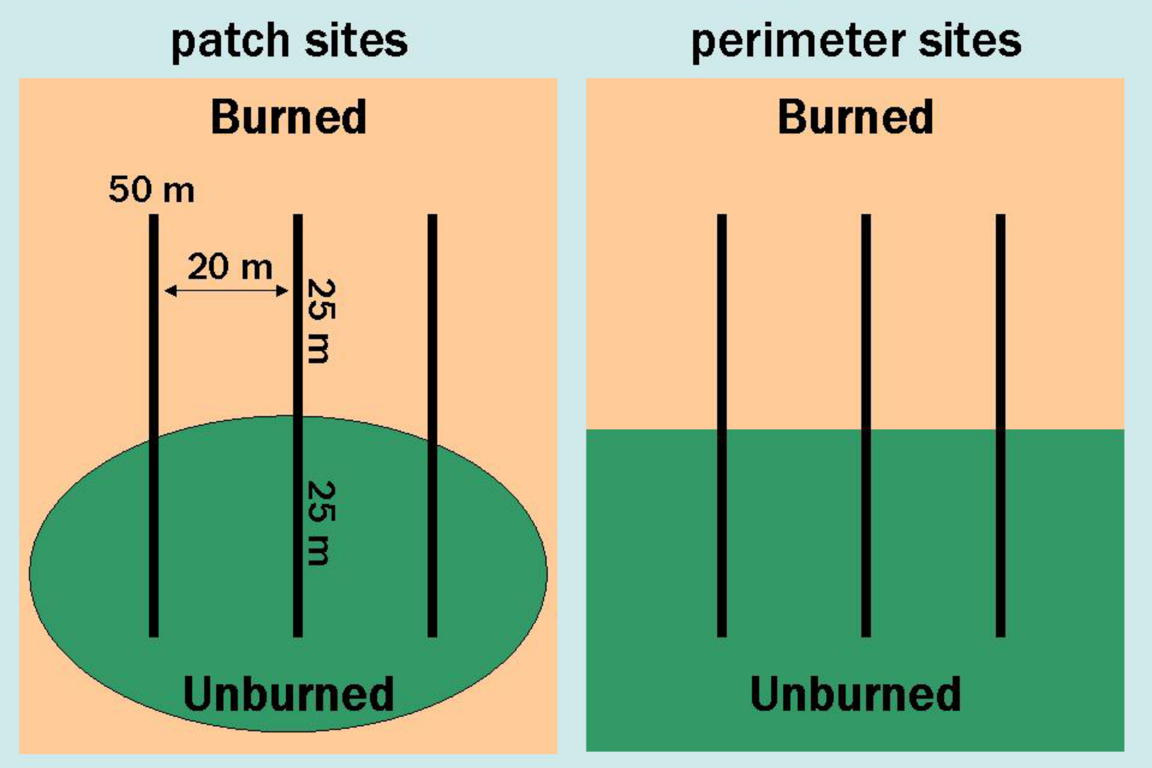


FIGURE 2. Transect design. Each site had three 50 m transects separated by 20 m. Half (25 m) of each transect was located in burned habitat and 25 m in unburned habitat.

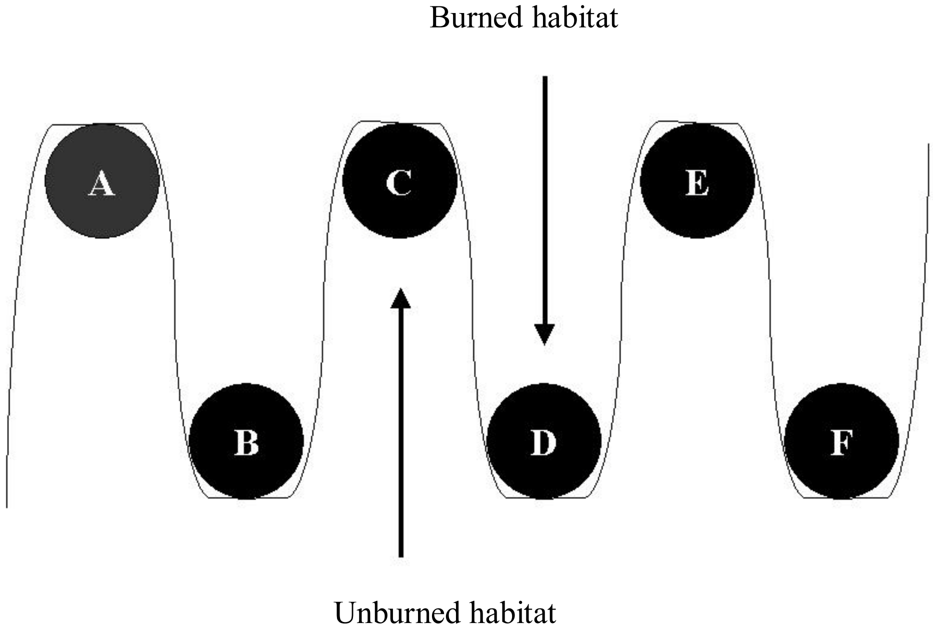


FIGURE 3. Pitfall array design. Buckets were fenced on three sides to prevent reptiles from the burned area entering traps A, C, and E and reptiles from the unburned area entering traps B, D, and F.

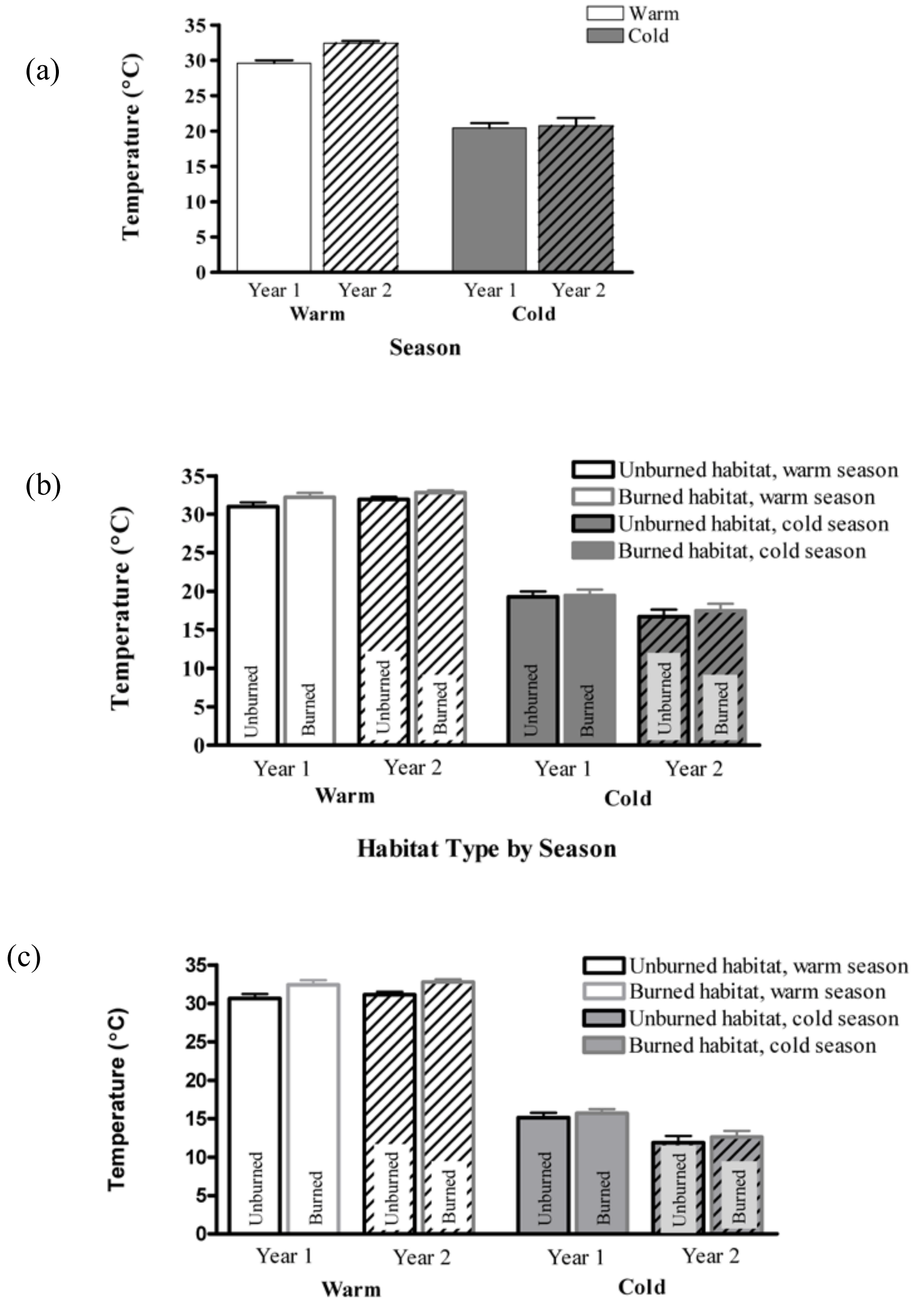


FIGURE 4. Ambient, ground, and subterranean temperatures ($\bar{x}$ ± SD). (a) Average ambient temperatures by year in the warm and cold seasons. (b) Average ground temperatures for unburned and burned habitats by year in each season. (c) Average subterranean temperatures for both habitats by year in each season.

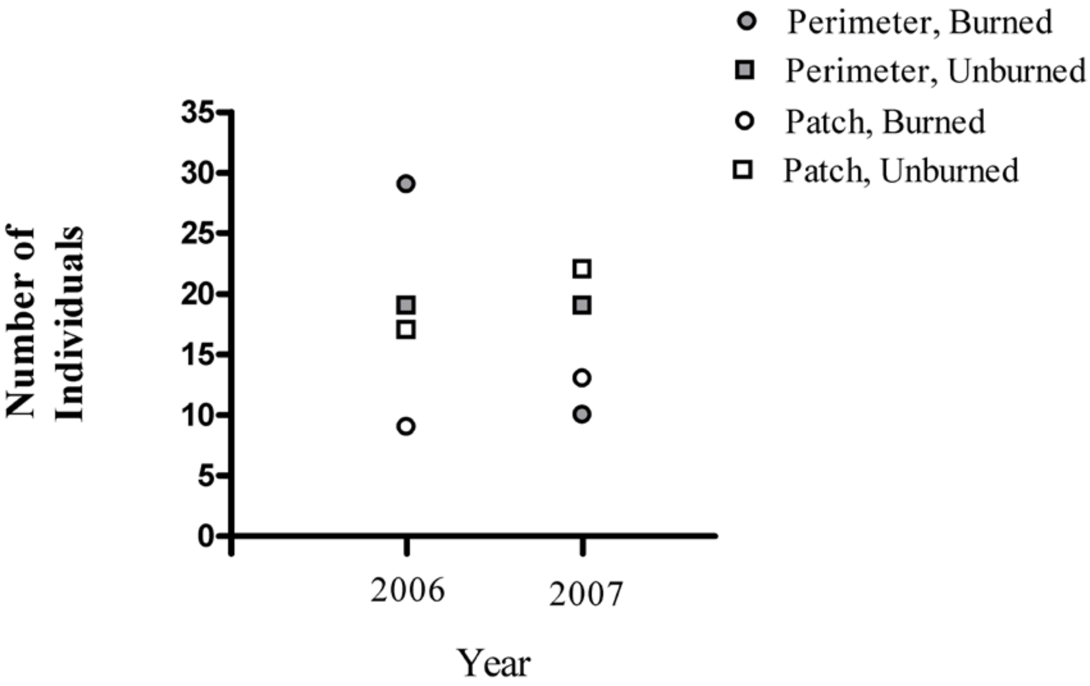


FIGURE 5. Total number of *Uta stansburiana* observed during transect surveys in each habitat type by year.

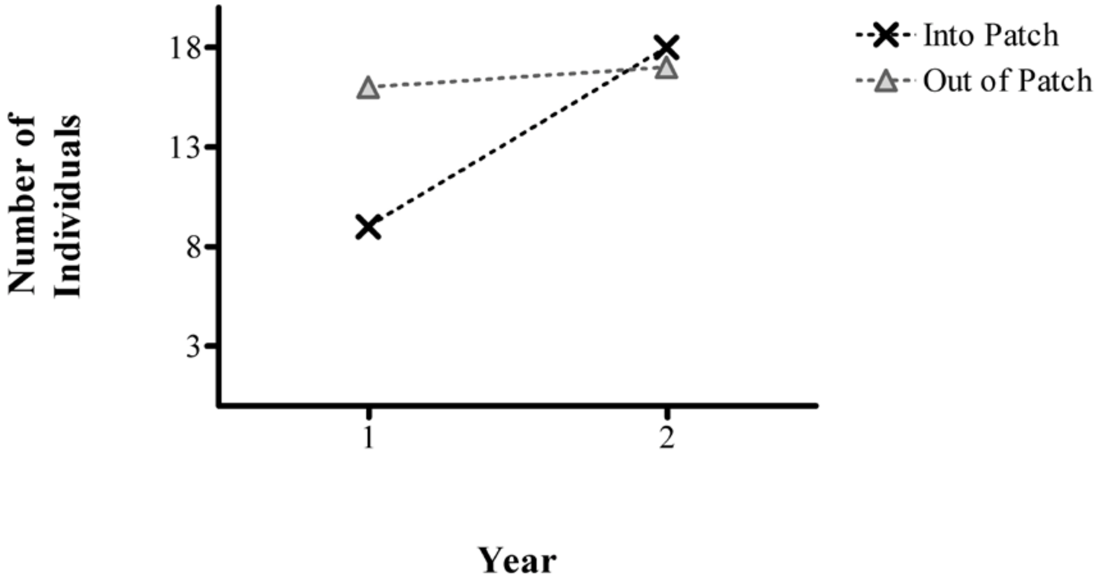


FIGURE 6. Total number of *Uta stansburiana* captured in pitfall traps moving into or out of habitat patches by year. Recaptured individuals were removed from the totals.

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Cite as: Brooks, M.L. and R.A. Minnich. *In Press*. Fire in the Southeastern Deserts Bioregion. Chp 16 in: Sugihara, N.G., J.W. van Wagtendonk, J. Fites-Kaufman, K.E. Shaffer, and A.E. Thode (eds.). Fire in California Ecosystems. University of California Press, Berkeley.

Fire in the Southeastern Deserts Bioregion

Matthew L. Brooks and Richard A. Minnich

Because of the inescapably close correlation between prevalence of fire and amount of fuel, deserts are characteristically less affected by fire than are most ecosystems … however, even though fire frequency and severity may be relatively low in any rating scale, their effect on the ecosystem may be extreme.
- Humphrey 1974, page 366.

Description of Bioregion

Physical Geography

The southeastern deserts bioregion (desert bioregion) occupies the southeastern 27% of California (110,283 km^2 or 27,251,610 acres) (Miles and Goudy 1997). The desert bioregion is within the basin and range geomorphic province of western North America, and includes two ecoregional provinces comprised of five ecological sections. The American Semi-Desert and Desert Province (hot-desert province) includes the Mojave Desert, Sonoran Desert, and Colorado Desert sections in the southern 83% of the desert bioregion (Table 16.1). The Intermountain Semi-Desert Province (cold desert province) includes the Southeastern Great Basin and Mono sections in the northern 17% of the desert bioregion.

Table 16.1. General descriptions and lightning frequencies (1985-2001) in the ecological sections of the southeastern deserts bioregion.

Ecological section[a]	% of bioregion	Constituent ecological zones[b]	Predominant Küchler vegetation types[c]	Lightning strikes/ 100km^2/yr[d]
Mojave	61	low, mid, high, montane, riparian	desert shrub 58% barren 37%	30
Sonoran	12	low, riparian	barren 82% desert shrub 18%	25
Colorado	10	low, mid, riparian	desert shrub 57% barren 38%	12
SE Great Basin	10	high montane, riparian	desert shrub 74% juniper-pinyon 18%	29
Mono	7	high, montane, riparian	sagebrush 46% juniper-Pinyon 15%	32

[a] Miles and Goudy (1997)
[b] low elevation desert shrubland, middle elevation desert shrubland and grassland, high elevation desert shrubland and woodland, desert montane woodland and forest, desert riparian woodland and oasis (see detailed descriptions in the text)
[c] potential natural vegetation types (Küchler 1964) that constitute 15% or more of the ecological section.
[d] Bureau of Land Management lightning detection data (van Wagtendonk and Cayan, in press)

The geomorphology of the desert bioregion is characterized by isolated mountain ranges with steep slopes separated by broad basins containing alluvial fans, lava flows, dunes, and playas. Elevations range from -85 m (-280 ft) below sea level in Death Valley, to 4,328 m (14,200 ft) above sea level in the White Mountains. Soil taxa range widely from hyperthermic or thermic, aridic Aridisols and Entisols in the Colorado, Sonoran, and Mojave Desert sections, to thermic, mesic, frigid, or cryic, aridic, xeric, or aquic Alfisols, Aridisols, Entisols, Inceptisols, Mollisols, and Vertisols in the Mono and Southeastern Great Basin sections (Miles and Goudy 1997). This wide range in geomorphology and soil conditions translates into a wide range of vegetation and fuel types, which include arid shrublands and semi-arid shrublands, grasslands, woodlands, and forests.

Climatic Patterns

Although frontal cyclones of the jet stream pass through the region during winter (November through April), virtually the entire desert bioregion is arid due to rain shadows of the Sierra Nevada, Transverse, and Peninsular ranges (Chapter 2, this volume). Precipitation locally increases with orographic lift in desert ranges, particularly those that rise above 2,000 m (6,096 ft). From July to early September, the region experiences 10 to 25 days of afternoon thunderstorms from the North American monsoon originating in the Gulf of California and Mexico. Thunderstorm cells tend to concentrate over high terrain, especially the eastern escarpments of the Sierra Nevada, Transverse, and Peninsular ranges, in the mountains of the eastern Mojave Desert, and in the high basin and range terrain between the White Mountains and Death Valley. The average annual precipitation on valley floors ranges from 10 to 20 cm (3.9 to 7.9 in) in the Mojave Desert and southeastern Great Basin, to 7 to 10 cm (2.8 to 3.9 in) in the Colorado and Sonoran deserts. The average annual rainfall total at Death Valley (5.8 cm, 2.3 in) is the lowest in North America. Precipitation increases to 20 to 30 cm (7.9 to 11.8 in) in the mountains above 2,000 m (6,562 ft), 40 cm (15.8 in) in the White Mountains, and 60 cm (23.6 in) in the upper leeward catchments of the Sierra Nevada, Transverse, and Peninsular ranges. The percentage of annual precipitation falling during summer (May through October) ranges from approximately 20% in the southeastern Great Basin to 40% at the Colorado River in the Sonoran Desert.

Interannual variation in rainfall is relatively high compared to other California bioregions, resulting in highly variable frequency and extent of fires among years. High rainfall produces fine fuels that promote fire spread, especially in the hot desert sections where fuels are otherwise sparse. Low rainfall causes shrub mortality which reduces woody fuel moisture and may promote fire spread in the cold desert sections where woody fuel cover is relatively high, although low fine fuel loads caused by low rainfall is probably more limiting to fire spread. Multi-decadal variation in rainfall has also been significant, with periods of relatively high rainfall from the turn of the century until 1946, a mid-century drought from 1947 to 1976, and a period of high rainfall 1977 to 1998 (Hereford et al. in press). This approximately 30-year cycle, coupled with below-average rainfall from

1999 to 2004, suggest that another 30-year drought period may be establishing, which could lead to reduced frequency and size of fires in most of the desert bioregion entering the 21st Century.

The entire desert bioregion has a large annual range of temperature due to its isolation from the stabilizing influences of the Pacific Ocean. There is also large regional variability due to variable elevational relief. Average January temperatures on valley floors range from -3 to 0° C (27 to 32° F) in the northeastern Great Basin to 7 to 10° C (45 to 50° F) in the Mojave Desert, and 11 to 13° C (52 to 55° F) in the Sonoran and Colorado deserts. Temperatures decrease with altitude to about 0° C (32° F) at 2,000 m (6,562 ft) and -8° C (18° F) at 3,000 m (9,842 ft.). During summer, average temperatures vary near the dry adiabatic lapse rate due to intense atmospheric heating in the absence of evapotranspiration under high rates of insolation. July average temperatures on valley floors range from 18 to 20° C (64 to 68° F) in the northeastern Great Basin to 25 to 30° C (77 to 86° F) in the Mojave Desert and 30 to 35° C (86 to 95° F) in the Sonoran and Colorado deserts. Maximum temperatures average > 40° C (104° F) below 1,000 m (3,281 ft) elevation and occasionally reach 50° C (122° F) in Death Valley, the Colorado River, and the Salton Sea trough. In the desert mountains, average temperatures decrease to 20° C (68° F) at 2,000 m (6,562 ft) and 10° C (50° F) at 3,000 m (9,842 ft). The decrease in temperature with altitude results in rapid decrease in evapotranspiration which in phase with increasing precipitation results in corresponding increase in woody biomass of ecosystems. Light snowpacks 10 to 15 cm (3.9 to 5.9 in) deep can develop in winter but typically disappear by spring above 2,000 m (6,562 ft), although deeper snow of 100 cm (39.4 in) can persist into the spring in subalpine forests > 3,000 m (9,842 ft).

Relative humidity during the afternoon in the summer fire season, when fires are most likely to spread, is very low throughout the desert bioregion. Average relative humidity in July ranges from 20 to 30% in the northeastern Mojave Deserts to 10 to 20% in the Mojave, Sonoran, and Colorado deserts. Values are low because moisture of the Pacific Coast marine layer is mixed aloft with dry subsiding air masses upon dissipation of the marine inversion, as well as from high temperatures produced by convective heating of surface air layers. The lowest humidity of the year (frequently < 10%) typically occurs in late June, just before the arrival of the North American monsoon.

Lightning frequency is higher in the desert than in any other California bioregion (van Wagtendonk and Cayan in press). Lightning strikes/100km^2/year averaged 27 (sd = 16) from 1985 through 2000, ranging from 32 in the Mono to 12 in the Colorado Desert sections (Table 16.1). The bioregions with the next most frequent lightning strikes were the Northeast Plateau (22 strikes/100km^2/year) and Sierra Nevada (20 strikes/100km^2/year). Most lightning in the desert bioregion occurred from July through September (78%), resulting from summer monsoons which developed in the Colorado, Sonoran, and eastern Mojave deserts, and from summer storms that developed in the Sierra Nevada mountains and drifted into the southeastern Great Basin and Mono sections. Lightning also occurred primarily during daylight hours, with 81% between 0600 and 1800.

Ecological Zones

From a fire ecology perspective, much of the variation in the desert bioregion relates to patterns of fuel characteristics and fire regimes. Vegetation (fuels), topography, and lightning strikes per unit area vary locally with elevation, and elevational vegetation gradients are correlated positively with latitudinal gradients and ecotones with more mesic regions in the immediate rain shadow of the Sierra Nevada, Transverse, and Peninsular ranges. Accordingly, we consider elevation to be the primary determinant of fire ecology zones in the desert bioregion. The ecological zones described below are listed in order of increasing elevation, except for the riparian zone, which transcends many of the other zones.

Low elevation desert shrubland zone

This is the predominant ecological zone in the Sonoran Desert section. Major vegetation types include alkali sink vegetation and the lower elevations of creosote bush scrub (Munz and Keck 1959) and succulent scrub (Rowlands 1980). Surface fuel loads and continuity are typically low, hindering the spread of fire (Fig 16.1).

Fig.16. 1. The low elevation desert shrubland ecological zone. This photo shows a creosotebush scrub vegetation typical of the Sonoran Desert.

Middle elevation desert shrubland and grassland zone

This is the predominant ecological zone in the Mojave Desert, Colorado Desert, and Southeastern Great Basin sections, where it typically occurs as an elevational band above the low elevation zone and below the high elevation zone. It also occurs at the regional ecotone between the Mojave and Great Basin deserts. Major vegetation types include Joshua tree woodland, shadscale scrub, the upper elevations of creosote bush scrub (Munz and Keck 1959), blackbrush scrub, and desert scrub-steppe (Rowlands 1980). Surface fuel characteristics are variable, but loads and continuity can be relatively high compared to the low elevation zone, facilitating the spread of fire (Fig. 16.2).

Fig. 16.2. The middle elevation desert shrubland and grassland ecological zone. This photo shows a blackrush scrubland, which typically includes blackbrush, Mojave yucca, Joshua tree, and California juniper.

High elevation desert shrubland and woodland zone

This is the predominant ecological zone in the Mono section. It also occurs at the tops of most Mojave Desert mountains or just below desert montane forests, and along the margins of the Sierra Nevada, Transverse, and Peninsular mountain ranges where they intergrade with yellow pine forests. Major vegetation types include sagebrush scrub, pinyon-juniper woodland, and desert chaparral (Munz and Keck 1959). Surface fuel loads and continuity are high where sagebrush scrub and chaparral dominate, facilitating the spread of fire. However, surface fuels are replaced by very high loads of crown fuels in closed pinyon-juniper woodlands, where fires only occur under extreme fire weather conditions and are typically very intense (Fig. 16.3).

Fig. 16.3. The high elevation desert shrubland and woodland ecological zone. This photo shows a pinyon-juniper woodland.

Desert montane woodland and forest zone

This zone is very limited in total area, and occurs almost exclusively in the Mono and Southeast Great Basin sections. Major vegetation types include bristlecone pine forest and alpine fell-fields (Munz and Keck 1959). Surface fuels are typically sparse, separating patches of crown fuels and hindering the spread of fire (Fig. 16.4).

Fig 16.4. The desert montane woodland and forest ecological zone. This photo shows a bristlecone pine forest.

Cite as: Brooks, M.L. and R.A. Minnich. *In Press*. Fire in the Southeastern Deserts Bioregion. Chp 16 in: Sugihara, N.G., J.W. van Wagtendonk, J. Fites-Kaufman, K.E. Shaffer, and A.E. Thode (eds.). Fire in California Ecosystems. University of California Press, Berkeley.

Desert riparian woodland and oasis zone.

This zone includes a diverse set of vegetation types that do not fit into any single elevational range. Vegetation types include oases and riparian woodlands, shrublands, grasslands, and marshes. Surface fuels loads and continuity can be very high, facilitating fire spread, although vertical continuity of ladder fuels and horizontal continuity of crown fuels are often insufficient to carry crown fires (Fig. 16.5).

Fig. 16.5. The desert riparian woodland and oasis ecological zone. This photo shows a riparian shrubland and woodland.

Overview of Historic Fire Occurrence

The primary factor controlling fire occurrence in the desert bioregion is fuel condition, specifically fuel continuity and fuel type. Where fuel continuity is low, as in most of the low elevation and desert montane ecological zones, fires will not typically spread beyond ignition points. Even where continuity is relatively high, fuelbeds may be comprised primarily of fuel types that do not readily burn except under the most extreme fire weather conditions. The coarse, woody fuels of pinyon-juniper woodlands in the high elevation ecological zone are a good example. Thus, variations in fuel condition are central to any attempts to evaluate past or current patterns of fire occurrence.

Prehistoric

Prehistoric fire regimes have not been quantitatively described for most of the desert regions of southwestern North America, largely because the usual tools for reconstructing fire histories, such as analyzing trees for fire scars or coring sediments in swamps or lakes for charcoal deposits, cannot be used where the requisite trees or lakes are not present. As a result, past fire regimes must be inferred indirectly from prehistoric vegetation studies or current observations and data.

Fossil packrat midden data suggest that most of the desert bioregion has been under arid to semi-arid conditions since the beginning of the Holocene (~10,000 years BP), with pinyon and juniper woodlands on upper slopes and at higher elevations, and low scrub and perennial grasslands in valleys and at lower elevations (Van Devender and Spaulding 1979, Koehler et al. 2005). Most interior basins in the desert bioregion did not support permanent lakes except those receiving runoff from the Sierra Nevada, Transverse, or Peninsular ranges. Thus, the major vegetation types that presently occur in the desert bioregion, and the ecological zones described in this chapter, were likely present in the desert bioregion throughout the Holocene, expanding and contracting relative to each other as they shifted up and down elevational gradients with periods of low and high rainfall.

The low elevation ecological zone probably contained low and discontinuous fuels, hindering fire spread and resulting in low intensity, patchy burns and long fire return intervals. Consecutive years of high rainfall would have increased fine fuel loads and continuity, and may have allowed fire to spread periodically in this ecological zone, especially were rainfall was highest along the western margins of the Mojave and Colorado deserts close to the Transverse and Peninsular mountain ranges.

The middle elevation, high elevation, and riparian zones likely had sufficient perennial plant cover to periodically carry fire in the prehistoric past without significant amounts of fine fuels. Because these fires would have been carried by relatively high cover of perennial shrubs and grasses, they were likely moderate intensity, stand replacing fires, as they typically are today.

Fuels in the desert montane zone were probably discontinuous resulting in small, patchy, and very infrequent surface or passive crown fires. Evidence of this is the presence of the long-lived (>3,000 years), but fire sensitive, bristlecone pine trees (*Pinus longaeva*).

It seems highly probable that fuel conditions and fire regimes have remained relatively constant across the desert bioregion during the Holocene, although their spatial distributions likely varied as the ecotones between vegetation formations shifted with alternating periods of low and high rainfall. Current climate conditions have generally persisted since ~1,440 years BP in the Mojave Desert (Koehler et al. 2005), supporting the supposition that relative distributions of fuel conditions and ecological zones have remained relatively constant during at least the latter part of the Holocene. It is also likely that fuel conditions and fire regimes have changed significantly since the late 1880s due to land use activities and invasions by non-native annual grasses. We discuss these changes in more detail below.

Historic

Livestock grazing can reduce perennial plant cover, especially cover of perennial grasses (Brooks et al. in press), which very likely has led to reduced landscape flammability since grazing began in the desert bioregion during the late 1880s. However, at the same time that fuels were reduced due to grazing, ignitions probably increased as fire came into use by livestock operators to convert shrublands into grasslands and increase forage production, especially in the Mono and middle to high elevations of the Southern Great Basin and Mojave sections. For example, rangelands in southern Nevada, southwestern Utah, and northwestern Arizona were extensively burned during the early 1900s to reduce shrub cover and promote the growth of perennial grasses (Brooks et al. 2003). Similar rangeland burns may have also been implemented in the southern and eastern Mojave Desert and the far western Colorado Desert, where summer rainfall occurs in sufficient amounts to support large stands of perennial grasses. However, most of the southern hot desert regions are too dry to support sufficient native fuels to carry fire, so even if ranchers tried to burn, they may have often been unsuccessful.

Analyses of historical aerial photos from 1942, 1953 to 54, 1968, 1971 to 74, 1998, and 1999 at Joshua Tree National Park indicate that there were periodic fires prior to 1942 (Minnich, 2003), during a 30-year period of relatively high rainfall that lasted until 1946 (Hereford et al. in press). However, most fires were <121 ha (300 acres) with the largest encompassing 607 ha (1,500 acres), and all occurred in the middle and high elevation ecological zones (Minnich, 2003). The spatial clustering of burns in some areas suggests that deliberate burning by humans was practiced, possibly to improve range production for livestock. During the mid-century drought, only three small fires occurred, all during the 1960s and in Joshua tree woodlands of the middle elevation ecological zone. Soon after the drought ended in 1977, fires again became more prevalent, but their size and numbers eclipsed what was observed prior to the mid-century drought. The first was a 2,428 ha (6,000 acre) fire in 1978, and the most recent was a 6,070 ha (15,000 acre) complex of fires that burned over a period of 5 days in 1999, both in the middle and high elevation ecological zones. These recent fires at Joshua Tree National Park were fueled largely by old stands of native trees, shrubs, and perennial grasses, but fire spread was additionally facilitated by stands of the non-native annual grasses red brome (*Bromus madritensis* ssp. *rubens*) and cheatgrass (*Bromus tectorum*), especially where fire passed through previously burned areas where cover of these grasses was especially high (National Park Service, DI-1202 fire reports).

Current

Records from land management agencies provide information on recent fires that can be used to reconstruct current fire regimes across the desert bioregion. We extracted data from fire occurrence records (DI-1202 reports) archived by the United States Department of the Interior and Department of Agriculture between 1980 and 2001 to create basic summaries for each of the five ecological sections in the California desert (Fig. 16.6, Table 16.2). This 21-year database is too short to capture the full range of potential burning conditions, because it was coincident with a period of above-average rainfall from 1977 to 1998 (Hereford et al. in press). However, it represents the best data available to approximate fire regimes since 1980 in the desert bioregion of California.

Table 16.2. Recent fire history (1980-2001)[a] in the ecological sections of the southeastern deserts bioregion.

Ecological section[b]	Total fires	Total Area burned	Fire frequency (fires/1000km^2/yr)	Annual area burned (ha/1000 km^2/yr)	Fire size (ha/fire)	Human: lightning fires	% of lightning strikes that resulted in fires[c]
Mojave	3158	69110	2.1	47	22	3.6	0.6
Sonoran	175	13217	0.6	47	76	7.5	0.2
Colorado	525	21340	2.2	88	41	44.2	1.8
Mono	1630	49292	9.6	292	30	0.5	2.0
SE Great Basin	90	5460	0.4	23	61	1.0	0.1
TOTAL	5578	158419	2.3	66	28	2.0	

[a] fire records (DI-1202 reports) of the Department of the Interior and Department of Agriculture, screened for errors as recommended by Brown et al. (2002).

[b] Miles and Goudy (1997)

[c] lightning frequency (van Wagtendonk and Cayan, in press) per lightning fires.

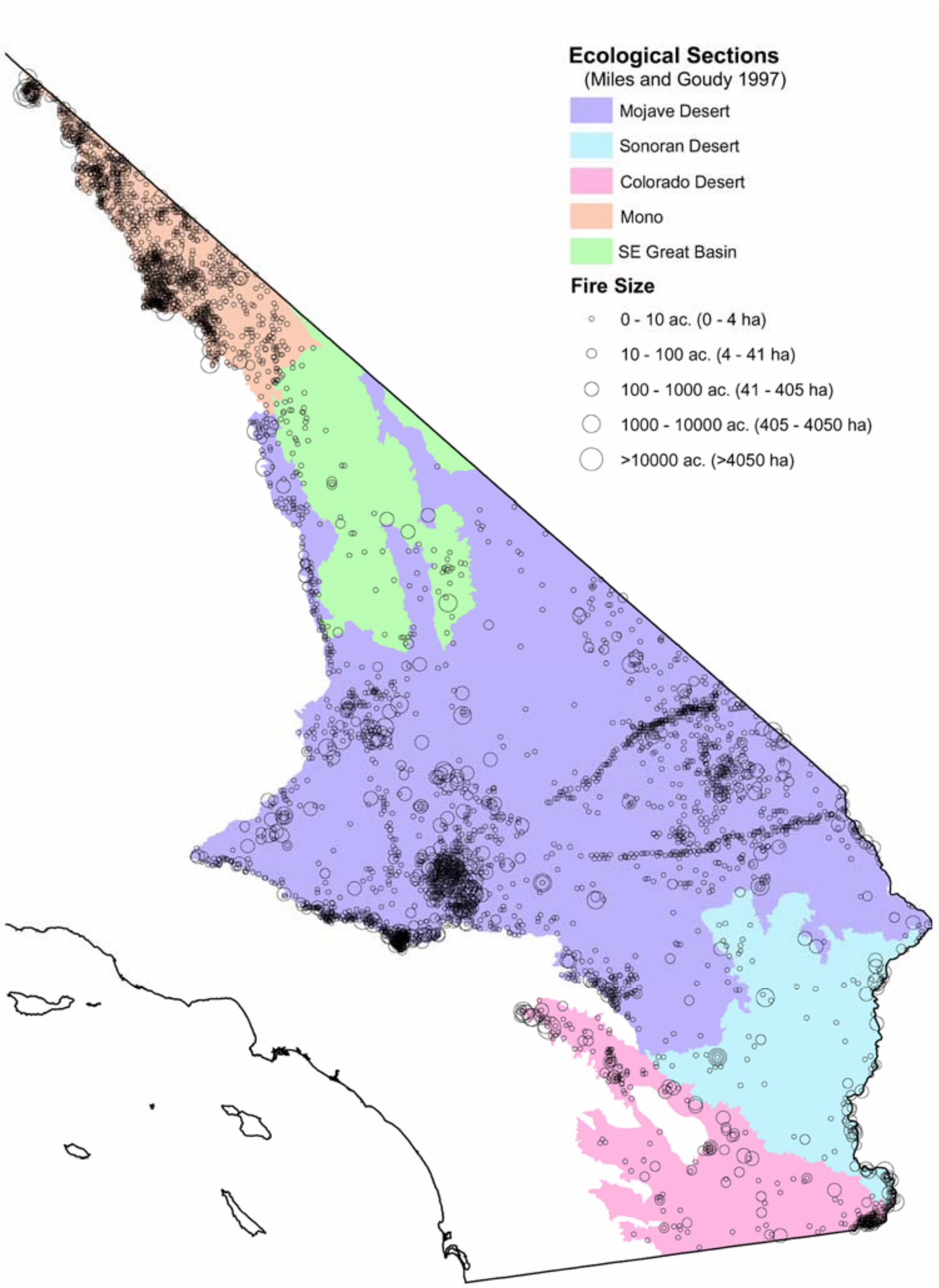

Fig. 16.6.Recent fire occurrences (1980-2001) in the five ecological sections of the Southeastern Deserts Bioregion.

Cite as: Brooks, M.L. and R.A. Minnich. *In Press*. Fire in the Southeastern Deserts Bioregion. Chp 16 in: Sugihara, N.G., J.W. van Wagtendonk, J. Fites-Kaufman, K.E. Shaffer, and A.E. Thode (eds.). Fire in California Ecosystems. University of California Press, Berkeley.

The primary message from these fire records is that the proportion of total area that burned per year from 1980 to 2001 is very small, peaking in the Mono section at 0.3%/yr (292 ha/1,000 km^2/yr, Table 16.2), resulting in a fire cycle of 342 years in that ecological section. The annual fire frequency and area burned were highest in the Mono section, and lowest in the southern Great Basin section (Fig 16.6, Table 16.2), peaking from May through September. Among the hot desert regions, fire frequency was highest in the Mojave and Colorado deserts, and the annual area burned was highest in the Colorado Desert. The percentage of lightning strikes that resulted in fire was highest in the Mono and Colorado Desert sections, probably due to high fuel continuity caused by the prevalence of sagebrush steppe in the Mono section, and red brome dominated creosote bush scrub in the western Colorado section. The Colorado Desert section had the highest ratio of human:lightning caused fires. This is probably due to both the high human population density and agricultural activity in the Coachella and Imperial valleys, and the low frequency of lightning in the Colorado Desert (Table 16.1). The northern cold desert regions had the lowest frequency of fires caused by humans, probably due to its remoteness from major human population centers.

In a separate analysis of agency fire data from 1980 to 1995 in the Mojave, Colorado, and Sonoran desert sections, fires were found to be clustered in regional hotspots (Brooks and Esque 2002), where they were much more frequent and burned more proportional area than the desert-wide averages indicated in Table 16.2. Annual fire frequency increased significantly from 1980 through 1995 ($r^2 = 0.27$) (Brooks and Esque, 2002), but the increase was only significant in the low and middle elevation zones below 1,280 m (4,200 ft) ($r^2 = 0.32$, 1980 to 2001) (M. Brooks, unpublished data). A few areas burned three separate times during this 15-year interval. The increase in fire frequency was due to increased number of fires caused by humans, since the number of lightning-caused fires remained constant (Brooks and Esque, 2002). Another major contributor to increased fire frequency was a general increase in fine fuel loads caused by heightened dominance of non-native annual grasses beginning in the late 1970s (e.g. Hunter 1991) and continuing on through the 1990s (M. Brooks personal observation), probably the result of above-average rainfall from 1976 to 1998 (Hereford et al. in press). Although most fires were small and started along roadsides, most of the large fires occurred in remote areas far from major roads, and were typically started by lightning (Brooks and Esque, 2002).

Major Ecological Zones

In this section we describe the basic fire ecology of the predominant plant species in each ecological zone. We also discuss patterns of postfire succession, and interactions between plant communities, fire behavior, and fire regimes. More details on the fire ecology of a wider range of desert species can be found in other recent publications (Brown and Smith 2000, Esque and Schwalbe 2002).

Low Elevation Desert Shrubland Zone

This zone includes two primary vegetation types. Alkali sink vegetation occurs on poorly drained saline and/or alkaline playas, flats, and fans approximately -80 to 1,200 m (-63 to 3,937 ft) throughout all the ecological sections. Plant communities include iodine bush-alkali scrub, allscale-alkali scrub, Mojave saltbush-allscale scrub, and saltgrass meadow (Rowlands 1980). Creosote bush scrub vegetation occurs 0 to 1,200 m (0 to 3,937 ft) on well-drained flats, fans, and upland slopes of the Mojave, Colorado, and Sonoran Desert ecological sections. However, only the lower elevations below about 900 m (2,953 ft), were perennial plant cover is relatively low, are typical of the low elevation desert shrubland zone. Plant communities include creosote bush scrub, cheesebush scrub, succulent scrub (Rowlands 1980).

Fire responses of important species

Most shrubs in the low elevation zone do not survive after being completely consumed by fire (Humphrey 1974, Wright and Bailey 1982) (Table 16.3), but since many fires in this zone are patchy and of low intensity, plants frequently survive in unburned islands. Low fire temperatures in interspaces, and high temperatures beneath woody shrubs, likely results in relatively higher seedbank mortality for annual plants that frequent beneath-shrub than interspace microhabitats (Brooks 2002). A few perennial species that evolved to resprout after natural flooding disturbances often resprout after burning, such as desert willow (*Chiloposis linearis*), catclaw (*Acacia greggi*), smoke tree (*Dalea spinosa*), and cheesebush (*Hymenoclea salsola*) (Table 16.3). Cheesebush can have almost 100% survival rates even after being totally consumed by fire (Table 16.4). Cacti are usually only scorched during fires, as flames propagate through their spines but the stems do not ignite due to their high moisture content. Individuals with high levels of scorching typically die from uncontrolled desiccation that occurs postfire. Cactus regeneration can occur from resprouting of partially scorched plants, or rooting of fallen unburned stem fragments, but less frequently from establishment of new seedlings.

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Table 16.3. Fire responses of some dominant plant species in the southeastern deserts bioregion.

	Predominant Type of Fire Response[1]		
Lifeform	Sprouting	Individual	Species
Conifer	none	killed	bristlecone pine, limber pine, pinyon pine, Utah juniper
Hardwood	fire stimulated	top-killed	shrub live oak, salt cedar*, honey mesquite, willows
	fire stimulated	underburned	Fremont cottonwood,
Shrub	fire stimulated	top-killed	catclaw acacia, smoke tree, desert willow, fourwing saltbush, cheesebush, rubber rabbitbrush, spiny hopsage, antelope bitterbrush
	none	killed	Shadscale, blackbrush, creososte bush, brittlebrush, white bursage, snakeweed, cliffrose
Stem and Leaf Succulents	none	killed	Cacti
	fire stimulated	top-killed	Mojave yucca, bananna yucca, Joshua tree[2]
Herb	fire stimulated	top-killed	bulbs
	none	killed	annual forbs
Grass	fire stimulated	top-killed	perennial grasses (e.g. Galleta grass, Indian ricegrass, desert needlegrass, fountain grass*)
	none	killed	annual grasses (e.g. red brome*, Mediterranean grass*, cheatgrass*, six-week fescue).

[1] varies depending on fire intensity and percentage of plants consumed

[2] after initially resprouting, Joshua trees often die within 5 years if most or all of their foliage was scorched or consumed

* non-native species

Table 16.4. Survival rates of perennial shrubs after being unburned (0% of living biomass burned), scorched (1-10% of living biomass burned) or consumed (11-100% of living biomass burned) during 2.25ha (5.6acre) fires in August 1995 at three low elevation shrubland sites (M. Brooks, unpublished data).

species[a]	sample size	% survival[b]			notes on fire behavior[c]
		year 1	year 4	year 8	
Central Mojave Site					
white bursage					Fire did not spread from ignition points. Therefore, the litter beneath each shrub, but not the shrub itself, was ignited. Most creosote bushes were consumed, because accumulated dead branches beneath them provided supplemental surface fuels that increased flame residency time beneath them, and ladder fuels that helped carry fire up into the creosote bush canopies.
unburned	n=20	100	100	85	
consumed	n=20	20	20	10	
creosote bush					
unburned	n=25	100	100	100	
scorched	n=4	25	25	25	
consumed	n=21	0	0	0	
Southern Mojave Site					
creosote bush					Fire spread rapidly from a few ignition points and burned 50% of the site. Few shrubs were consumed due to low fuel loads beneath creosote bushes, and low cover of finely textured sub-shrubs.
unburned	n=25	100	100	100	
scorched	n=13	77	70	62	
consumed	n=12	8	8	8	
Western Mojave Site					
white bursage					Fire spread slowly from multiple ignition points, and burned 50% of the site. Most shrubs were consumed due to high fuel loads beneath creosote bushes and the presence of many finely textured sub-shrubs.
unburned	n=10	100	100	90	
consumed	n=10	20	20	20	
cheesebush					
unburned	n=10	100	100	60	
consumed	n=10	100	100	80	
creosote bush					
unburned	n=25	100	100	100	
scorched	n=8	88	75	75	
consumed	n=17	12	12	12	
Anderson wolfberry					
unburned	n=20	100	100	90	
scorched	n=5	100	100	80	
consumed	n=20	75	75	50	

[a] Dominant perennial plant species at each site. Not all were represented by both scorched and consumed plants. white bursage = *Ambrosia dumosa*, creosote bush = *Larrea tridentata*, cheesebush = *Hymenoclea salsola*, Anderson wolfberry = *Lycium andersonii*.

[b] Shrub survival was defined as possessing live leaf tissue, either on unburned or resprouted stems, when sampled during May of 1996, 1999, and 2003.

[c] Additional descriptions of the fires and study sites are reported in Brooks 1999.

The most frequently encountered and dominant shrub in this zone, creosote bush (*Larrea tridentata*), can have 25 to 80% survival rates 8 years postfire when it is only scorched (1 to 10% biomass loss), and 0 to 12% survival rates by year 8 when it is consumed by fire (11 to 100% biomass loss) (Table 16.4). Individuals with slight to moderate scorching displayed 30 to 40% survival in the Sonoran Desert in Arizona (Dalton 1962), and in general, fire intensity and duration is inversely correlated with sprout reproduction (White 1968).

The wide range in survival rates among creosote bushes appears to be associated with their variable physiognomy and variable fuel loads beneath their canopies and across the landscape, which translate into variable fire intensity and vertical continuity from surface to canopy fuels. Individuals with canopies in the shape of inverted cones tend to occur in water-limited environments (De Soyza et al. 1997), resulting in relatively low fuel loads beneath their canopies and across the landscape and a relatively low probability of being completely consumed by fire. In contrast, individuals with hemispherical canopies that extend to the ground tend to occur in less water-limited environments (De Soyza et al. 1997), resulting in higher fuel loads beneath their canopies and across the landscape and a higher probability of being completely consumed by fire. Resprouting in creosote bushes also probably varies throughout the extensive range of this species, especially at ecotones with vegetation types that support more frequent burning. For example, moderate (O'Leary and Minnich 1981, Brown 1984) to high (Brown 1984) rates of postfire resprouting were reported at the ecotone of the western Colorado Desert with shrubland vegetation in the Peninsular ranges.

Fire regime-plant community interactions

This is the zone that Humphrey (1974) was primarily referring to when he stated that in desert shrublands "…fires are a rarity, and the few fires that do occur cause little apparent damage to the various aspects of the ecosystem…" (pp. 337). This is largely because fuels are discontinuous and characterized by a sparse 8 to 15% cover of woody shrubs, and the large interspaces between shrubs are mostly devoid of vegetation, inhibiting fire spread (Fig. 16.1). A recent summary of fire regimes of the United States (Schmidt et al. 2002) assumed that Küchler's "barren vegetation type" (Küchler 1964), which covers most of the low elevation desert shrubland zone, is mostly devoid of vegetation and therefore fireproof. However, 9% of fires and 7% of the total area burned between 1980 and 2001 occurred within the barren vegetation type in the California desert bioregion. Thus, fires do occur in the low elevation desert shrubland zone, although not as frequently and over less area than in the other zones of the desert bioregion.

Fire behavior and fire regimes in this zone are affected primarily by the ephemeral production of fine fuels from annual plants. Years of high winter and spring rainfall can increase continuity of fine fuels by stimulating the growth of annual plants that fill interspaces and allow fire to spread (Brown and Minnich 1986, Schmid and Rogers 1988, Rogers and Vint 1987, Brooks 1999). Native annuals that produce some of the most persistent fuelbeds include the annual grasses six-weeks fescue (*Vulpia octoflora*) and small fesue (*Vulpia microstachys*), and the large forbs fiddleneck (*Amsinckia tessellata*), tansy mustard (*Descurania pinnata*), and lacy phacelia (*Phacelia tanacetifolia*), compared to a whole suite of smaller native forbs (119 species, Brooks 1999). Infrequently, successive years of high rainfall may have allowed these native annuals to build up fine fuel loads sufficient to carry fire across the interspaces between larger perennial plants. Low elevation fires carried by high loads of native annuals typically only burn dead annual plants and finely-textured sub-shrubs, leaving many of the larger woody shrubs such as creosote bush unburned. Thus, the historic fire regime was likely characterized by relatively small, patchy, low intensity surface fires, and a truncated long fire return interval (Table 16.5).

Table 16.5. Fire regime classification for desert shrubland zones.

Desert shrubland zone	*Vegetation Type*			
		Low elevation shrubland	Middle elevation shrubland and grassland	High elevation shrubland and woodland
	Temporal			
	Seasonality	Spring-summer-fall	Spring-summer- fall	Summer-early fall
	Fire Return Interval	Truncated long	Long	Long
	Spatial			
	Size	Small	Moderate to large	Moderate to Large
	Complexity	High	Multiple	Low to Moderate
	Magnitude			
	Intensity	Low	Moderate	Moderate to High
	Severity	Moderate	Moderate to high	High
	Fire Type	Surface	Passive crown to active crown	Active crown

The invasion of non-native annual grasses into the desert bioregion introduced new fuel conditions. Species such as red brome and Mediterranean grass (*Schismus arabicus* and *S. barbatus*) provide more persistent and less patchy fine fuelbeds than do native annual plants, breaking down more slowly and persisting longer into the summer and subsequent years (Brooks 1999). These new fuel conditions have the potential to increase the size, decrease the complexity, and shorten the time interval between desert fires, although fire intensity will likely decrease because fine herbaceous non-native fuels are replacing coarse woody native fuels. These fire regime changes have occurred over a small fraction of the low elevation ecological zone, and fire regimes over the vast majority of this zone still are within the historical range of variation.

Mediterranean grass is the most widespread and abundant non-native annual grass in the low elevation shrubland zone, although red brome may predominate under large shrubs or in the less arid parts of this ecological zone. Mediterranean grass has fueled fires as large as 41 ha (100acres) (Bureau of Land Management DI-1202 records), and interspace fuel loads of as little as 112kg/ha (100 lbs/acre) are sufficient to carry fire (Brooks 1999). Because these fires burn with low intensity, soil heating is negligible and most woody shrubs are left unburned.

The recent spread of Sahara mustard (*Brassica tournefortii*) throughout the low elevation shrublands has caused concern that this invasive mustard may introduce a significant new fuel type to the desert bioregion. During years of high rainfall this invasive annual can exceed 1 m (3.3 ft) in height with a rosette of basal leaves 1 m (3.3 ft) across, and even moderately sized plants can produce as many as 16,000 seeds (M. Brooks unpublished data). Plants can remain rooted and upright through the summer fire season, and when they finally do break off they blow like a tumbleweed and lodge in shrubs or fencerows, accumulating piles of fuels similar to Russian thistle (*Salsola* spp.). There are no records of fires specifically caused by Sahara mustard in the desert bioregion, however, the combination of this species with red brome in the understory helped fuel a 20.2 ha (50 acre) fire in creosote bush scrub in northwest Arizona (M. Brooks, personal observation). During the 5 years after this fire, Sahara mustard and red brome have come to dominate this site while the native creosote bush has yet to show signs of recovery.

Non-native annual plants that evolved in other desert regions will likely be most successful at persisting in the California desert bioregion. For example, Mediterranean grass and Sahara mustard respectively evolved in the arid Middle East and Northern Africa, and they have also successfully established in the desert bioregion (Brooks 2000, Minnich and Sanders 2000). At three sites in the western Colorado Desert, these non-native species successfully persisted through two major droughts, which occurred during the end of the 1980s and 1990s (R. Minnich, unpublished data). Their cover values in 1983, 1988, and 1990 through 2001 were comparable or higher than those of the non-native forb red-stemmed filaree (*Erodium cicutarium*), which is a poorer fuel source for fires (Brooks 1999), and compared to all native forbs combined.

Middle Elevation Desert Shrubland and Grassland Zone

This zone includes five primary vegetation types. The upper elevations of creosote bush scrub that generally occur at 900 to 1,200 m (2,953 to 3,937 ft) and contain higher perennial plant cover than the lower elevations of this vegetation type. Joshua tree woodland occurs on well-drained loamy, sandy, or fine gravelly soils of mesas and gentle slopes from 760 to 1,300m (2,493 to 4,265 ft) in the Mojave Desert and Southeastern Great Basin sections. Shadscale scrub occurs on heavy, rocky, often calcareous soils with underlying hardpan from 1,000 to 1,800m (3,281 to 5,906 ft) in the Mono, Southeastern Great Basin, and Mojave Desert sections. Blackbrush occurs on well drained, sandy to gravelly often calcareous soils from 1,000 to 2,000m (3,281 to 6,562 ft) in the southern Mono, Southeastern Great Basin and Mojave Desert sections. Desert scrub-steppe vegetation types are intermixed with a wide range of other plant communities from the low to the high elevation ecological zones, but they are most common in the middle elevation zone. Indian ricegrass scrub-steppe and desert needlegrass scrub-steppe typically occur were winter rainfall predominates within creosote bush scrub (Rowlands 1980). Big galleta scrub-steppe typically occurs in creosote bush scrub below 1,000 m (3,281 ft), and in Joshua tree woodland and blackbrush scrub above 1,000 m (3,281 ft).

Fire responses of important species

Higher fuel loads and more continuous fuelbeds in the middle elevation ecological zone result in higher intensity fires and higher frequency of top-killing in plants than in the low elevation zone. However, more species in this zone are likely to resprout after being top-killed. Perennial grasses such as desert needlegrass (*Achnatherum speciosa*), galleta grass (*Pleuraphis rigida* and *P. jamesii*), and Indian ricegrass (*Achnatherum hymenoides*) readily resprout after burning (Table 16.3). Spiny menodora (*Menodora spinescens*) and joint-fir (*Ephedra* spp.) often survive fire because their foliage does not readily burn. In contrast, some shrub species such as blackbrush (*Coloegyne ramosissima*) and winterfat (*Kraschennikovia lanata*) rarely survive burning.

Blackbrush is one of the more flammable native shrubs in the desert bioregion, due to its high proportion of fine fuels and optimal packing ratio. In the rare case that only a portion of a shrub is consumed, it may survive and resprout from the root crown. This resprouting was observed within the first few postfire years (Bates 1984), and these resprouts were still evident 20 years later (M. Brooks personal observation), at a site in the Mono section near Bishop, California. It is commonly thought that blackbrush stands take centuries to recover (Bowns 1973, Webb et al. 1988). However, analyses of historical photographs from Joshua Tree National Park and southern Nevada indicate that blackbrush stands can recover within 50 to 75 years (Minnich 2003, M. Brooks unpublished data), although other historical photographs from other locations do not indicate recovery within this time interval (M. Brooks, unpublished data). It seems probable that the ability of blackbrush to resprout after burning varies across its wide geographic range which extends from the Colorado Plateau and southern Great Basin on through the Mojave Desert.

Yucca species such as Joshua tree (*Yucca brevifolia*), Mojave yucca (*Yucca schidigera*), banana yucca (*Yucca baccata*), and Our Lord’s candle (*Yucca whipplei*) are typically scorched as flames propagate through the shag of dead leaves that line their trunks. The relatively small size and more optimal packing ratio of dead Joshua tree leaves compared to dead Mojave or banana yucca leaves, increases the frequency at which they are completely burned. This may partly explain why Joshua trees are more frequently killed by fire. All four yucca species readily resprout after fire, but Joshua tree resprouts are often eaten by herbivores or otherwise die soon after burning. Postfire recruitment of new Joshua trees is infrequent, and likely occurs during years of high rainfall. No seedlings or saplings were observed in burns <10 years old, and only <10 individuals/hectare were present on burns >40 years old in Joshua Tree National Park (Minnich 2003). Joshua tree populations along the extreme western edge of the desert bioregion often resprout and survive more readily after fire than those further east (M. Brooks personal observation). A cycle of relatively frequent fire and resprouting can result in short, dense clusters of Joshua tree clones, such as those found near Walker Pass, in the western end of the Antelope Valley, and in pinyon-juniper woodlands at ecotones with the Transverse ranges. High resprouting rates of Joshua trees in these areas may have evolved in local ecotypes that became adapted to relatively high fire frequencies at the ecotone between the desert bioregion and more mesic ecosystems to the west.

Fire regime-plant community interactions

Some of the most continuous native upland fuels in the desert bioregion occur at the upper elevations of this zone, especially in areas dominated by blackbrush (Fig. 16.2). Invasive annual grasses have contributed to increased fire frequencies since the 1970's (Brooks and Esque, 2002), although the native perennial vegetation in this zone can at times be sufficient alone to carry fire during extreme fire weather conditions (Humphrey 1974). Between 1980 and 2001, 49% of all fires and 45% of total area burned occurred in Küchler's desert shrubland vegetation type, which is roughly analogous to the middle elevation ecological zone.

At the lower elevations within this zone, where creosotebush is co-dominant with a wide range of other shrubs and perennial grasses, fire spread is largely dependent on high production of fine fuels filling interspaces during years of high rainfall (Brown and Minnich 1986, Schmid and Rogers 1988, Rogers and Vint 1987, Brooks 1999). At higher elevations within this zone, where blackbrush is often the primary dominant plant, fire spread is not so dependent on the infilling of shrub interspaces during years of high rainfall and fire occurrence does not vary as much inter-annually compared to lower elevations (M. Brooks unpublished data). Thus, the historic fire regime was likely characterized by relatively moderate to large sized, patchy to complete, moderate intensity, surface to crown fires, and a long fire return interval (Table 16.5).

The post-fire response of plant communities in blackbrush scrub is illustrative of the general responses of other desert scrub communities in the middle and high elevation ecological zones. Blackbrush fires remove cover of woody shrubs which is soon replaced by equivalent cover of herbaceous perennials and annual plants (Brooks and Matchett 2003). Alien species such as red brome, cheatgrass, and red-stemmed filaree typically increase in cover after fire, but only if rainfall is sufficient to support their growth and reproduction. Recovery of blackbrush stands may occur within 50 years (Minnich 2003, M. Brooks, unpublished data), but perhaps more typically take over 100 years (Webb et. 1988, Bowns 1973).

Red brome is the dominant invasive grass at middle elevations in the California desert bioregion. This invasive grass produces higher fuel loads and fuel depths than does Mediterranean grass, and accordingly produces longer flame lengths that carry fire into the crowns of large woody shrubs more readily, producing more intense fires (Brooks 1999). Cover of red brome can become greater and more continuous after fire, promoting recurrent fire (Sidebar 16.1, this volume). This positive invasive plant/fire regime cycle (*sensu* Brooks et al. 2004) has shifted fire regimes outside of their historical range of variation in some regional hotspots (Brooks and Esque 2002), although fire regimes in most of the middle elevation zone are probably similar to historical conditions.

The recent invasion of the non-native annual grass African needlegrass (*Stipa capensis*) into the ecotone between the Colorado Desert and the Peninsular ranges in the 1990s has helped fuel at least one 243 ha (600 acre) fire (R. Minnich, personal observation). There are early indications that this species can survive relatively dry years, suggesting that it may spread and become another source of fine fuels that may further alter fire regimes in the desert bioregion.

High Elevation Desert Shrubland and Woodland Zone

This zone includes three primary vegetation types. Sagebrush scrub occurs in 1,100 to 2,800 m (3,600 to 9,186), although it can extend to 3,800 m (12,467 ft) in the White Mountains. Pinyon-juniper woodland occurs 1,300 to 2,400 m (4,265 to 7,874 ft), and can reach 2,700 m (8,858 ft) in the White Mountains. Both vegetation types occur in the Mono, Southeastern Great Basin, and Mojave sections. Among the pinyon-juniper vegetation types, the Utah juniper – single-leaf pinyon association is the most widespread, occurring in the Mono, Southeastern Great Basin, and eastern Mojave Desert ecological sections of California (Minnich and Everett 2001). The California juniper – single-leaf pinyon association occurs along the desert slopes of the Transverse ranges at the edge of the Mojave Desert section, with California juniper dominating below 1,700 m and single-leaf pinyon dominating above. Desert chaparral is the least prevalent of the major vegetation types in this ecological zone. It occurs on the middle slopes of the Transverse ranges adjacent to the Mojave Desert, and the Peninsular ranges adjacent to the Colorado Desert, below the mixed conifer forests, and in the same general elevation range as sagebrush scrub and pinyon-juniper woodland.

Fire responses of important species

Relatively high fuel loads result in high fire intensity, but plant mortality rates can vary widely among species. Wyoming big sagebrush (*Artemisia tridentate* ssp. *wyominensis*) is typically killed by fire, but it often re-establishes readily from wind-dispersed seeds. Cliffrose (*Purshia mexicana*) is typically killed by fire, whereas its close relative, antelope bitterbrush (*Purshia tridentata*), exhibits highly variable responses to fire, sometimes resprouting (Table 16.3). Interior chaparral species, such as *Quercus cornelius-mulleri, Q. turbinella, Cercocarpus betuloides, Arctostaphylos glauca,* and *A. glandulosa, Nolina* spp., either resprout or reseed soon after fire, but lower rainfall and sparser vegetation cover results in less frequent fire and slower recovery rates than is typical of cis-montane chaparral.

Pinyon pine (*Pinus monophylla*, *P. edulis*) and juniper (*Juniperus osteosperma*, *J. californica*) are typically killed by fire, but these woodlands can re-establish after 100+ years of fire exclusion. Juniper typically re-establishes from seed sooner than pinyon pine. Initial establishment of single-leaf pinyon pine appears to be delayed 20 to 30 years by sun scald and/or freeze/thaw soil heaving until the establishment of the shrub layer and young juniper trees which act as nurse plants (Wangler and Minnich 1996). The first pinyon recruits establish within the canopies of nurse plants, often near root axes. The establishment of a pinyon pine canopy after about 75 years eventually reduces freeze-thaw processes, setting off a chain-reaction of spatially random recruitment throughout old burns. Pinyons develop complete canopy closure after 100 to 150 yr which is accompanied by a decline in the surface vegetation, due apparently to shrub senescence and shade stress.

Fire regime-plant community interactions

Fuel continuity is similar to that of the middle elevation zone, but the fuels are generally more woody and difficult to ignite. In addition to high plant cover, the prevalence of steep slopes in this ecological zone facilitates the spread of fire. Due to the high biomass of woody fuels created by juniper and pinyon pine, and to a lesser extent sagebrush (*Artemisia* spp.), bitterbrush, cliffrose, and scrub oak (*Quercus turbinella*), the fires that do start are among the most intense encountered in the desert bioregion. Between 1980 and 2001, 33% of fires and 45% of the total area burned occurred in Küchler's sagebrush, juniper-pinyon, and chaparral vegetation types which are characteristic of the high elevation ecological zone.

Fire spread can occur most any year in sagebrush steppe, although it is more likely when fine fuel loads (especially cheatgrass and red brome) are high following years of high rainfall, or during periods of high winds and low relative humidity. Fires are patchy to complete, moderate intensity passive crown to crown fires, depending the continuity of the woody shrub fuels. Fire spread in pinyon-juniper woodlands is most probable when live fuel moisture and relative humidity are low and winds are high. When fires did historically occur, they were mostly large, intense crown fires, burning through woodland crown fuels. At the interface between sagebrush steppe and pinyon-juniper woodland, a surface to passive crown fire regime is the norm, as fire spreads through woody and herbaceous surface fuels and occasionally torches woodland fuels, especially younger trees. The historic fire regime was likely characterized by relatively large, patchy to complete, moderate intensity surface to crown fires, and a long fire return interval (Table 16.5).

Sagebrush stands generally require 30 to 100 years to recover following fire (Whisenant 1990). Where cheatgrass has dramatically shortened fire return-intervals, especially in the lower elevation Wyoming big sagebrush communities, sagebrush steppe has been converted to non-native annual grassland (Sidebar 16.1, this volume). In the higher elevation mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities, this type conversion is much less common, since the native shrubs and perennial grasses recover much more rapidly after fire.

Fire suppression coupled with removal of fine fuels by livestock grazing has allowed pinyon-juniper woodlands to encroach on sagebrush steppe across much of the western United States (Miller and Tausch 2001), including the Mono section of the desert bioregion. However, it is less likely that woodland encroachment has occurred in the more arid hot desert regions, due to low primary productivity rates. Recent resampling of 1929 to 1934 California Vegetation Type Map (VTM) survey plots reveal no significant changes in woodland densities at the western edge of the hot desert regions (Wangler and Minnich

1996). Pinyon-juniper woodlands adjacent to the Transverse ranges have experienced long periods between stand-replacement fires both before and after fire suppression began (fire rotation periods, ~450 years; Wangler and Minnich 1996).

Fires in pinyon-juniper woodlands are least frequent in open stands at lower elevations and more frequent in dense forests at higher elevations, in response to changing productivity and fuel accumulation gradients with increasing elevation and rainfall. The upper elevation ecotones between pinyon-juniper woodlands and mixed conifer forest are typically very narrow, due to truncated disturbance gradients related to fire behavior and stem mortality (Minnich 1988). The thin bark of pinyon pine prevents their survival in the frequent surface fire regime typical of mixed conifer forests. Alternatively, postfire surface fuels appear to lack sufficient biomass to support short-period burns, and as canopy closure occurs in pinyon and juniper woodlands, surface fuel loads and continuity are further reduced. Thus, a historical discontinuity in fire return intervals probably existed along the ecotones between mixed conifer forests and pinyon woodlands in which understory surface fires at high elevations shift to long-period stand-replacement crown fires at lower elevations in response to differences in stand structure, fire behavior, and tree survivorship (Minnich 1988).

Desert Montane Woodland and Forest Zone

There are two primary vegetation types in this ecological zone. Bristlecone-limber pine forests occur on well-drained, shallow, dolomitic soils from 2,600 to 3,800 m (8,530 to 12,467 ft) in the Inyo, White, Panamint, Funeral, and Grapevine mountains. Alpine fell-fields occur above timberline, primarily in the White Mountains. Small white fir forest enclaves also occur on north-facing slopes from 1,900 to 2,400m (6,234 to 7,874 ft) in the New York, Clark, and Kingston mountains of the Mojave Desert section (Rowlands 1980).

Fire responses of important species

The flagship tree species of this ecological zone, bristlecone pine and limber pine (*Pinus flexilis*), have thin bark which makes them susceptible to mortality during fires (Table 16.3). Although most individuals are struck by lightning by the time they are 1,000 years old, strikes may not result in the entire tree burning, since many old individuals have scars resulting from multiple lighting strikes. The presence of ancient bristlecone pine individuals is testimony to the historical infrequency of fire. As a result, most plant species in this zone are not adapted to recovery from fire, although species associated with other periodic natural disturbances such as from colluvial erosion may be able to resprout after burning.

Fire regime-plant community interactions

Fuels are very discontinuous, but in contrast to the low elevation zone, ephemeral production by annuals during years of high rainfall adds very little to the fuel bed, due to shallow soils, low temperatures, and a short growing season. As a result, surface fires are extremely rare, and most fires that do occur spread through the crowns of pines only during extreme fire weather conditions, but even these fires are very small <1ha (2.5 acres). Between 1980 and 2001, <1% of all fires and total area burned occurred in Küchler's great basin pine, alpine meadows-barren, and mixed conifer vegetation types characteristic of the desert montane ecological zone.

Low productivity results in very low fuel loads and continuity in the desert montane forests. Except on steep, north-facing canyons, heavy fuels are widely spaced and fine fuels are low and relatively unflammable, making it difficult to carry fire in this landscape. Thus, the historic fire regime is characterized by truncated small, patchy, variable intensity, passive crown fires, and a truncated long fire return interval (Table 16.6).

Table 16.6. Fire regime classification for the desert montane woodland, and riparian woodland/oasis zones.

Desert montane woodland, and riparian woodland/oasis zone	*Vegetation Type*		
		Desert montane woodland	Riparian woodland/oasis zone
	Temporal		
	Seasonality	Summer-early fall	Spring-summer-fall
	Fire Return Interval	Truncated long	Short to moderate
	Spatial		
	Size	Truncated small	Small to moderate
	Complexity	Moderate	Low
	Magnitude		
	Intensity	Multiple	High
	Severity	Multiple	Multiple
	Fire Type	Passive Crown	Passive to active crown

Desert Riparian Woodland and Oasis Zone

Riparian woodlands occur primarily along the Colorado and Mojave river corridors adjacent to low elevation shrublands in the southern desert region. Other examples can be found in the Amargosa Gorge, Whitewater River, Andreas Canyon, and Palm Canyon. In the northern desert region, riparian woodlands occur along the Owens and Walker rivers and the many creeks along the east slope of the Sierra Nevada Mountains. Oasis woodlands occur in isolated stands such as the Palm Canyon, Thousand Palms, and Twentynine-palms oases in the Colorado Desert section.

Fire responses of important species

Woodland dominants such as Fremont cottonwood (*Populus fremontii*) honey mesquite (*Prosopis glandulosa*), and willows (*Salix* spp.) typically resprout after being topkilled (Table 16.3). However, resprouting individuals and seedlings are susceptible to mortality during recurrent fires. Oasis species such as Washington fan palm (*Washingtonia filifera*) benefit from frequent, low-intensity fire, which reduces competition for water from other plants growing at the surface, and allow new seedlings to become established.

Fire regime-plant community interactions

Fuel characteristics and fire behavior are extremely variable, due to the wide range of vegetation types that characterize the riparian zone. In general fuels are typically continuous and fuel loads high, but fuel moisture content is also often high. Fires may not carry except under extreme fire weather conditions. Thus, the historic fire regime is characterized by small to moderate sized, complete, high intensity passive to active crown fires, and a short to moderate fire return interval (Table 16.6).

In riparian woodlands the invasives saltcedar (*Tamarix* spp), and less frequently giant reed (*Arundo donax*), create ladder fuels that allow fire to spread from surface fuels of willow (*Salix* spp.), saltbush (*Atriplex* spp.), sedge (*Carex* spp.), reed (*Juncus* spp.), and arrow weed (*Pluchea sericea*) into the crowns of overstory Fremont cottonwood trees, top-killing them. After an initial fire, these invasive quickly recover and surpass their pre-fire dominance, promoting increasingly more frequent and intense fires which, can eventually displace most native plants (Sidebar 16.2, this volume).

In palm oases, Washington fan palms depend on surface fire to clear understory species and facilitate recruitment. However, these sites can be pre-empted by saltcedar as it rapidly recovers after fire. The ladder fuels saltcedar creates can also carry fire into the crown of Washington fan palms, increasing the incidence of crown fires (Sidebar 16.2, this volume)

Cite as: Brooks, M.L. and R.A. Minnich. *In Press*. Fire in the Southeastern Deserts Bioregion. Chp 16 in: Sugihara, N.G., J.W. van Wagtendonk, J. Fites-Kaufman, K.E. Shaffer, and A.E. Thode (eds.). Fire in California Ecosystems. University of California Press, Berkeley.

Management Issues

Fuels Management

The deserts of southwestern North America are one of the fastest growing regions in terms of human populations in the United States. As human populations increase, so to do the number of people living at the wildland-urban interface, which complicates fire management in many ways (Chapter 19, this volume). Increasing human populations can also potentially change fuel characteristics, through increased air pollution which can increase deposition rates of atmospheric nitrogen, and potentially increase fine fuel loads (Brooks 2003). Burgeoning human populations can also increase the introduction rates of new plant species that could add new fuel components and fire hazards to the region (Chapter 22, this volume). Since fire spread is mostly limited by the availability of contiguous fuels, fuel management can be a very important tool for fire managers in the California desert bioregion, even though the areas in which it is used may be a small percentage of the total region.

Herbaceous fuel management

The fuel component of greatest concern in the desert bioregion is the continuous cover the non-native annual grasses red brome, cheatgrass, and Mediterranean grass that appear during years of high rainfall. Although populations of these non-native annual plants and their resultant fine fuel loadings wax and wane with annual and multi-decadal fluctuations in rainfall (Sidebar 16.1, this volume), they have changed fire behavior and fire regimes in many parts of the desert bioregion, especially in the low elevation ecological zone where their presence is almost a prerequisite for large fires.

Despite all the concern surrounding the non-native species already dominating the desert bioregion, new grass invaders such as fountain grass (*Pennisetum setaceum*), buffelgrass (*Cenchrus ciliare*), and African needlegrass, and invasive mustards such as Sahara mustard, may pose additional fire hazards in the future. For example, in the Sonoran Desert, buffelgrass invasion coupled with frequent fire has converted desertscrub to non-native grassland in Mexico (Búrquez et al. 2002), created fuels sufficient to carry fire in Arizona, and recently appeared in southeastern California (M. Brooks personal observation). Land managers who once lamented the damage caused by fires fueled by red brome in southern Arizona are even more concerned now about the potential effects of buffelgrass (S. Rutman, Organ Pipe Cactus National Monument, personal communication). Buffelgrass is currently being considered for addition to the Arizona Department of Agriculture, Noxious Weed List, due primarily to its ability to alter fire regimes (E. Northam, personal communication). Thus, fine fuels management should be closely tied to invasive plant management, because the predominant plant invaders in the southern part of the desert bioregion are relatively flammable herbaceous species (Brooks and Esque, 2002). This is important both from the perspective of managing invasive plant fuels that are currently present, and preventing the establishment of new invasive plants that may change fuel structure and potentially cause even greater fire management problems in the future.

Livestock grazing has been mentioned as a possible tool for managing fine fuels in the desert bioregion (Brooks et al. 2003, Minnich 2003). It may temporarily reduce fine fuel loads, and be effective for managing fuels in specific areas such as within the wildland urban interface. However, grazing may also reduce cover of late seral native plants and replace them with non-native annual and other early seral plant species (Brooks et. al 2003) that can be more flammable. Grazing treatments must be applied with attention to the potential responses of all dominant plant species, both in the short term based on the phenologic stage during which they are grazed, and in the long term based on their life history characteristics and inter-relationships among species.

Woody fuel management

Where native plant cover is sufficient to carry fire without the addition of fine fuels from non-native plants, coarse woody fuels are the major concern of fire managers. In the central and southern parts of the desert bioregion, blackbrush intermixed with perennial grasses, Joshua trees, and juniper produce the right mix of high fuel continuity, fuel loads, and fuel packing ratio that can cause large intense fires with frequent spotting ahead of the flaming front. Although infrequent, intense, stand-replacing fires are a natural part of blackbrush shrubland ecology, these types of fires are not desirable when they occur near human habitations, or where they may damage cultural resources such as historical buildings or pre-historical sites. Once these fires start, they often require indirect firefighting tactics to suppress, which complicates efforts to protect specific areas from burning. As a result, land managers and scientists are testing ways to reduce the chances of extreme fire behavior in this vegetation type where it occurs between Joshua Tree National Park and the communities of Yucca Valley and Joshua Tree (M. Brooks et al., unpublished data). They are comparing the effects of fire and mechanical blackbrush thinning on subsequent fuel conditions, fire behavior, and plant community structure. The goal is to find tools that will allow managers to manipulate fuel characteristics to reduce fire hazards near areas identified for protection from fire, while having minimal negative ecological effects, such as increased dominance of invasive non-native plants.

Sagebrush and pinyon-juniper fuels are the primary focus of fuel management in the northern parts of the desert bioregion, especially in the Mono section. Sagebrush intermixed with perennial grasses is generally considered to be a greater fire hazard than the blackbrush communities described above. A century or more of fire exclusion, livestock grazing, and climate change can also result in encroachment by pinyon-juniper woodlands into sagebrush steppe (Miller and Tausch 2001). This has been documented in the northeast bioregion of California (Schaefer et al. 2003), and has also occurred where rainfall is relatively high in the desert bioregion at the ecotone of the Great Basin desert with the Sierra Nevada Mountains (Anne Halford, botanist, BLM-Bishop Field Office). Dense stands of mature trees in that area increase the chance of intense, stand-replacing, crown fire. Unfortunately, these same mature woodlands are desirable for use as homesites, especially in the Mono section, complicating the implementation of fuels management treatments and the protection of homes during fires. Millions of hectares are planned for fuels reduction in the western United States (http://www.fireplan.gov), and much will involve thinning of smaller size classes of pinyon and juniper trees to allow surface fuels to increase, and moderate intensity surface fires to return to the ecotone between pinyon-juniper woodlands and sagebrush steppe. Because very little is known about the effectiveness of these treatments in changing fire behavior or the potential ecological effects of these treatments, a research project was recently begun to quantify the effects of pinyon and juniper thinning on subsequent fuel condition, fire behavior, and ecosystem variables at a site in northwestern Arizona (M. Brooks et al., unpublished data).

Where sagebrush and pinyon-juniper vegetation interface in the southern desert sections, they are either at high elevations far from major roads and human habitations, or they contain surface fuels of insufficient amount and continuity to carry fire. These stands only burn under extreme fire weather conditions. Analyses of aerial photographs and VTM survey data from the 1930s show no evidence of pinyon-juniper expansion in the southern parts of the California desert region (R. Minnich, unpublished data). Accordingly, management of pinyon-juniper fuels is not advisable in this region, except were needed for specific cultural resource or safety reasons.

Fire Suppression

There is specific concern about the effect of fire suppression activities on the federally threatened desert tortoise where it occurs in low and middle elevation zones (Sidebar 16.3, this volume). More generally, fire suppression in desert wilderness areas became a significant issue after the California Desert Protection Act (1994) applied this designation to many new areas. Wilderness areas often encompass mountain ranges in the desert bioregion, where locally high fuel loads from both native and non-native plants, and steep slopes, facilitate the spread of fire. Fire suppression options are generally more limited in these areas by the constraints outlined in wilderness management plans, and often the primary tactic is to wait for fire to spread down slope and attempt to stop it along pre-existing roads. This can result in large portions of desert mountain ranges burning during a single event. The question is, which causes greater ecological damage, activities associated with aggressive fire fighting (e.g. construction of hand or bulldozer control lines, fire retardant drops) or large-scale, sometimes recurrent, fire occurring where fires were historically small and infrequent? We recommend that suppression be a high priority where fire frequency has been recently high in regional hotspots and non-native grass fire cycles have become locally established (Brooks and Esque 2002), where local populations of non-native plants may be poised to expand their range and landscape dominance following fire (mostly in the middle elevation ecological zone), or where there are other management reasons to exclude fire. Otherwise, a let burn policy for natural fires may be appropriate.

Postfire Restoration

Burn Area Emergency Rehabilitation (BAER) teams have developed postfire restoration/rehabilitation plans after the large fires that have recently occurred in the Mono section (e.g. Cannon and Slinkard fires), and further south in the desert bioregion at its ecotone with the Transverse and Peninsular ranges (e.g. the Juniper Complex and Willow fires). Much of this effort is focused on protecting watersheds from soil erosion, and one of the common tools is the seeding of rapidly growing plants (Sidebar 20.1, this volume). In general, seeding treatments establish more readily in the cold deserts than in the hot deserts, although relative establishment rates and the ecological effects of seeding in these two regions have not been experimentally compared.

Postfire seeding may also be used to compete with and reduce the cover of invasive grasses associated with the grass-fire cycle (Sidebar 16.1, this volume). The idea is to replace highly flammable species such as cheatgrass with less flammable seeded species. Non-native perennial grasses such as crested wheatgrass (*Agropyron desertorum*) have been used to compete with and reduce cover of cheatgrass in Great Basin sagebrush steppe. However, there has been a recent move toward using native species in postfire seeding, which may not have the same effect as non-native perennial grasses in suppressing the growth of non-native annual grasses such as cheatgrass. A current study is evaluating the relative effectiveness of non-native versus native perennial grasses to compete with and reduce cover of cheatgrass after fires in sagebrush steppe in the Mono section, and at sites in the Great Basin and Colorado Plateau (M. Brooks, unpublished data).

Fire Management Planning

One of the biggest challenges in fire management planning is determining desired future conditions to use as management goals. In cases where historical fire regimes can be reconstructed (e.g. ponderosa pine forest), the natural range and variation of historical fire regime characteristics may be a realistic and appropriate target. However, management goals may be elusive where historical fire regimes cannot be easily reconstructed, such as in the desert bioregion where one must rely on indirect inferences.

Fire histories alone may not be enough to establish management goals when protection of specific natural or cultural resources are the primary management goal, or where plant invasions have changed the rules of the game. For example, if plant invasions have shifted fuel characteristics outside of their natural range of historical variation, then restoration of historical fire regimes may be impossible without first dealing with the invasive plants that are at the root of the problem (Brooks et al. 2004). Although it appears that fire regimes, and at least woody fuel conditions, across much of the desert bioregion may be within their historical range of variation, it is difficult to quantify the impact that non-native plant invasions have had, aside from recognizing that fire regimes have been altered dramatically in some regional hotspots (Brooks and Esque 2002). Further complicating this process are the effects of potential future changes in rainfall patterns (Hereford et al. in press), and levels of atmospheric CO^2 (Mayeaux et al. 1994) and nitrogen deposition (Brooks 2003), on fuel conditions and fire regimes. All of these potential variables need to be considered when determining fire management goals in the desert bioregion.

The recent mandate by federal land management agencies to create fire management plans for all management units has resulted in a flurry of activity as new plans are drafted and old plans are revised. In many cases, plans developed for desert management units are supported by relatively few scientific studies, due to the paucity of fire research that has been conducted in the desert regions of North America. Decisions on when and where fuels should be managed, fires should be suppressed or allowed to burn, or post-fire restoration projects should be implemented, are difficult to make given the limited data available. Recent reviews have attempted to provide land managers and others with current information on desert fire ecology and management (Brooks and Pyke 2001, Brooks and Esque 2002, Esque and Schwalbe 2002, Esque et al 2002, Brooks et al. 2003). Along these same lines, a primary purpose of this desert bioregion chapter is to provide additional information that can be used in the development of fire management plans in the deserts of southwestern North America.

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SIDEBAR 16.1. Ecological Effects of Non-native Annual Grasses

by Matthew Brooks and Richard Minnich

Non-native annual grasses in the genera *Bromus*, *Avena*, and others have become dominant components of many grasslands, shrublands, woodlands, and forests in western North America during the 20th century. These invasions have negatively affected native plant species by directly competing with them for limiting soil nutrients and water, and by altering ecosystem properties such as fuel characteristics and fire regimes. The positive feedback between non-native grass dominance and increased fire frequency, or the "grass/fire cycle" (D'Antonio and Vitousek 1992), is the most clearly understood and well-documented example of the more general "invasive plant/fire regime cycle" (Brooks et al. 2004).

Fire frequencies that have increased beyond their historical range and variation can have dramatic and far-reaching ecological effects. For example, invasion of the non-native cheatgrass (*Bromus tectorum*) has altered fuelbed characteristics and shortened fire return intervals from 30 to 100 years to 5 years in areas of the Great Basin (Whisenant 1990). This new fire regime promotes the dominance of cheatgrass over native species, resulting in large-scale conversions of high diversity, native sagebrush steppe to low diversity, non-native annual grassland. This vegetation change has negatively affected animals that require sagebrush steppe for forage and cover such as the sage grouse (*Centrocercus urophasianus*) (Sidebar 11.2, this volume), and prey species such as black-tailed jackrabbits (*Lepus californicus*) and the Paiute ground squirrel (*Spermophilus mollis*) which are important for golden eagles (*Aquila chrysaetos*) and prairie falcons (*Falco mexicanus*) (Knick and Rotenbery 1995, Knick et al 2003). Although similar large-scale higher-order effects have not been documented in the Mojave, Colorado, or Sonoran deserts, non-native grass/fire cycles have degraded habitat for the desert tortoise (*Gopherus agassizii*) in localized hotspots within these desert regions (Brooks and Esque 2002, Sidebar 16.3 this volume).

Invasive plant/fire regime cycles represent ecosystem shifts to alternative stable states which will likely persist unless fuels, climate, or ignition patterns significantly change (Brooks et al. 2004). For example, non-native annual grasses such as cheatgrass and medusahead (*Taeniatherum caput-medusea*) persist in cold desert regions like the Great Basin because rainfall is typically sufficient to support reproduction during any given year. Although the fuelbeds they create may only significantly affect fire behavior following years of high rainfall, their populations will likely persist even during years of low rainfall. As a result, non-native grasses and the altered fire regimes they cause are now relatively permanent features in many parts of the cold desert region.

In contrast, the hot desert regions of the Mojave, Colorado, and Sonoran deserts receive less annual rainfall than the cold desert regions, increasing the chances of population crashes of non-native annual grasses such as cheatgrass and red brome (*Bromus rubens*). Rainfall events as small as 5 mm (2 in) can stimulate their germination, and when there is little subsequent rainfall, the plants often die before reproducing (M. Brooks and R. Minnich, personal observations), potentially depleting the soil seedbank. This is probably why red brome became locally extinct at two low elevation desert sites after the late 1980s drought, and at one low elevation site after the late 1990s drought (R Minnich, unpublished data). However, extirpation of red brome did not occur at many higher elevation desert sites following these same drought periods (M. Brooks, personal observation). Broad-scale responses by non-native grasses to droughts indicate that they are typically not regionally extirpated and can recover to ecologically significant numbers relatively quickly in hot desert regions. For example, after the end of the approximately 30-year mid-century drought (Hereford et al. in press) red brome density and biomass jumped 700% and 150% respectively between the last year of the drought (1975) and the first year of higher rainfall (1976), and by 1988 the increase above 1975 levels reached 15,646% for density and 1,596% for biomass at a Mojave Desert/Great Basin ecotone in southern Nevada (Hunter 1991). During this time interval, density and biomass of native annuals decreased (Hunter 1991), while the frequency and size of fires across the Mojave Desert steadily increased (Brooks and Esque 2002,). In addition, the shorter 1987-1991 drought was followed in 1993 by one of the biggest fire years in the 1980-2001 agency fire record for the hot desert regions, and the spread of many of these fires was facilitated by substantial fine fuebeds of red brome and cheatgrass.

Thus, non-native annual grasses will not likely ever become extirpated from the hot desert regions under the current climate regime, although their landscape dominance and effects on fire frequency and behavior will undoubtedly continue to be highly episodic in response to rainfall. Non-native grass/fire cycles have already become established in some localized hotspots within the hot desert region (Brooks and Esque 2002). The extent of area affected by these vegetation and fire regime type-conversions may expand during periods of high rainfall in the future, although most of this expansion will probably be confined to the middle elevation desert shrubland and grassland ecological zone. Below the middle elevation zone, extreme drought conditions will cause more frequent population crashes of red brome and cheatgrass and thus limit their influence on fire regimes, and above the middle elevation zone native woody plants and perennial grasses are the primary factors affecting fire regimes.

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SIDEBAR 16.2. Saltcedar Invasions Can Change Riparian Fire Regimes

by Tom Dudley and Matthew Brooks

Saltcedar (*Tamarix ramossissima*) was brought to North America in the early 1800's by European colonists as a horticultural plant, and by the early 1900's it became widely used to provide windbreaks and erosion control along railways and other erosion-prone sites. Its ability to tolerate periodic drought and harsh soil conditions helped insure its establishment persistence where other species failed. It was recognized as an invader of desert watercourses around the 1920's, and with the advent of water control and diversion projects took advantage of the altered conditions to expand its range during the middle and latter part of the century (Robinson 1965).

Saltcedar is deciduous and produces a fine-structured, water-repellent litter layer that is highly flammable in late summer and fall. Because stand densities can be very high, and litter is slow to decompose, a nearly-continuous layer of surface fuels can develop which carries fire throughout the stand (Busch and Smith 1992). The standing trees are also flammable, and can carry fire from surface fuels up into the canopies of native riparian trees. These fuel characteristics can create a frequent, high intensity, crown fire regime where an infrequent, low to moderate intensity, surface fire regime previously existed. After burning, saltcedar stump-sprouts readily and benefits from nutrients released by fire, whereas native riparian plants such as cottonwood and willow do not resprout as vigorously (Ellis 2001). Recurrent high intensity fire may lead to monoculture stands of saltcedar. Thus, saltcedar has turned many watercourses from barriers of fire movement to pathways for fire spread.

As stands of saltcedar increase in density and cover, native cottonwood and willow trees decrease. In some cases this is coincident with changing environmental conditions that do not favor the native species (e.g. decreased water tables caused by water diversion projects; Everitt 1998), but in other cases it is clear that saltcedar is responsible for the decline in native trees, directly through competition and indirectly through altered fire regimes (Busch and Smith 1995). Because it provides lower quantity and quality of shade, forage, and insect prey species, wildlife generally avoid large stands of saltcedar in preference for native stands (Shafroth et al. in press). This includes numerous threatened and declining riparian birds which find better nesting and feeding resources on native trees. In addition, saltcedar can have higher evapotransporation rates than native trees, potentially reducing water tables (Sala et al. 1996). All of these symptoms of saltcedar invasion have caused major management problems in southwestern riparian ecosystems.

Mechanical and chemical methods are typically used to manage saltcedar, however they can be very expensive ($300 - $6,000/ha.; Shafroth et al. in press), their effectiveness is often limited and temporary, and they can have other undesirable ecosystem effects. After more than a decade of pre-release testing, a leaf-feeding beetle from Eurasia, *Diorhabda elongata*, has been experimentally released in several western states as a biological control agent against saltcedar (Dudley et al. 2000). At one site in northern Nevada this beetle defoliated approx. 2 ha in 2002, and spread to defoliate over 400 ha in 2003. The physiological stress experienced by defoliated plants may lead to lowered live fuel moisture, and definitely increases the amount of dead wood and foliage. In the short term, this biocontrol may increase the chance of high-intensity fire, but in the long run the conversion of saltcedar stands back to native riparian woodlands will likely reduce fire hazards.

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SIDEBAR 16.3. Fire Effects on the Desert Tortoise (Gopherus agassizii)

by Matthew Brooks and Todd Esque

Changing fire regimes threaten 12 of the 40 major tortoise species worldwide (Swingland and Klemens 1989). Only general habitat destruction is listed as a threat for more species (23 of 40 species). In general, tortoises are poorly adapted to fire because they evolved in arid or semi-arid habitats where fire was historically rare. The desert tortoise (*Gopherus agassizii*), Mojave population, is a Federally Threatened species listed partly because of threats posed by fire.

Fires can kill desert tortoises, especially fires that occur in the spring and early summer when they are most active above-ground throughout their range (Esque et al. 2002). Years of high rainfall produce the profuse annual plant growth that is required for desert tortoise reproduction, but it also contributes to fire occurrence, especially at the low and middle elevation zones within the desert tortoise range. Thus, years when growth and reproduction are expected to be greatest can be coincident with increased fire occurrence. Although, mortality from individual fires is generally considered insignificant for wildlife populations compared to the habitat changes that can follow, loss of a few individuals may be catastrophic for local populations of species that are already in decline (Esque et al. 2003).

Fires can also affect desert tortoises indirectly, by changing habitat structure and plant species composition. Loss of cover sites that provide protection from the sun and predators, and loss of native forage plants are specific examples of the potential negative effects of fire (Brooks and Esque 2002, Esque et al. 2002). Individual fires may have relatively small indirect effects within desert tortoise habitat, since they are often patchy, leaving unburned islands of native vegetation. In contrast, recurrent fires pose a much greater threat, as they often burn through previously unburned islands of vegetation, and can produce broad landscapes devoid of shrub cover and dominated by non-native annual grasses. These conditions are currently focused within a number of regional hotspots in the desert bioregion (Brooks and Esque 2002).

When fighting fires that occur within desert tortoises habitat in the low and middle elevation zones, land managers follow guidelines developed to reduce the chance of killing desert tortoises such as not burning out unburned habitat islands when feasible, checking under tires before moving vehicles, and walking ahead of vehicles when they are required to travel off-road (Duck et al. 1998). Results of firefighting activities in desert tortoise habitats have proven that the benefit of fighting fires in desert tortoise habitat far outweighs the potential danger of damage to habitats and tortoise populations when appropriate guidelines are followed (Duck et al. 1998).

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FIRE EFFECTS ON SEED BANKS AND VEGETATION IN THE EASTERN MOJAVE DESERT: IMPLICATIONS FOR POST-FIRE MANAGEMENT

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INTRODUCTION

Limited information is currently available on the short-term effects of fire on soil seed banks and vegetation in the Mojave Desert. This information is critical for determining if postfire seedings are potentially beneficial, or even necessary, in this ecosystem. Of all the management tools, aerial seeding is potentially the most cost-effective over large areas because it requires the least amount of lead time. There are clearly many questions associated with this technology, but the more immediate question is whether seeding treatments are necessary in the first place. This question hinges on understanding the short-term effects of fire on the abundance and species composition of soil seed banks and germinated plants immediately following the 70,736 acre Hackberry Fire Complex which occurred at the Mojave National Preserve in the eastern Mojave Desert during late June 2005. Support for this project was provided by the Joint Fire Science Program (project #06-1-2-02).

METHODS

Six sites in the Hackberry Fire Complex were used as replicate sampling blocks, each containing one burned and one unburned experimental unit with 5 non-overlapping sampling units randomly established inside each. This randomized blocks study design consists of 6 blocks X 2 fire treatments X 5 sampling units = 60 total sampling plots. Sampling plots were set up in October 2005 and consisted of a 5 x 30m FMH brush belt transect (USDI National Park Service 2003), overlaid with a 20 x 50m modified Whittaker plot (Stohlgren et al. 1995). Burn severity measurements were collected on the brush belt transects, following FMH protocols (USDI National Park Service 2003). Four 6cm diameter x 3cm deep (volume = 85cm^3) soil samples were collected at each corner of the brush belt transect for determination of seed bank density and species richness and composited into a single soil sample. A ½ cup (111cm^3) portion was grown in a greenhouse during winter 2005-06 following methods adapted from Brenchley and Warington (1939) and modified by Young and Evans (1975). Seed bank density and species richness were measured by counting the number of germinated seedlings for each species.

Above-ground density, cover, and species richness of herbaceous and woody plants were measured during the phenological peak for annual plants in April and early May, 2006, following National Park Service FMH protocols (USDI National Park Service 2003). Spatially nested modified-Whittaker plots were used to measure plant species richness at 1, 10, 100, and 1,000m^2 scales. We focus specifically on the results of the seed bank and herbaceous plant sampling.

Data was analyzed as a randomized blocks analysis of variance (ANOVA) statistical model. The predictor variable was fire (burned, unburned). The response variables included seed bank density by groups of plants (non-native, native), above-ground vegetation density by groups, and species diversity of the seed bank and above-ground vegetation. The data was log transformed since it was not normally distributed and analyzed with SAS Proc GLIMMIX.

RESULTS AND DISCUSSION

Seed banks

Total seed bank density was significantly lower in burned (2,494 seeds/m^2) than unburned (12,460 seeds/m^2) areas ($P<0.0001$)(Fig. 1). This translates into a seed bank depletion (mortality) rate of 80%. Recent aerial seedings of postfire landscapes in the Mojave Desert have ranged from 140 seeds/m^2 (13 seeds/ft^2)(Christiana Lund, BLM, pers. comm.) to 646 seeds/m^2 (60 seeds/ft^2) (Karen Prentice, BLM, pers. comm.), and postfire drill seedings are typically applied at a rate of 323 seeds/m^2 (30 seeds/ft^2)(Karen Prentice pers. comm.). If these seeding rates were applied after the Hackberry Fire Complex, they would have only reduced the depletion rate of the seed bank to 79% if 140 seeds/m^2 were added, or 75% if 646 seeds/m^2 were added. To completely ameliorate seed bank depletion rates (to a 0% net loss), 9,966 seeds/m^2 (926 seeds/ft^2) would have to have been added, an increase of 1,543% over the highest aerial seeding rates typically used.

Non-native seed densities (dominated by *Erodium cicutarium*) were significantly lower in burned (345 seeds/m^2) than unburned (5,667 seeds/m^2) areas ($P<0.0001$)(Fig. 1) (94% depletion rate). Native seed densities were also significantly lower in burned (2,012 seeds/m^2) than unburned (6,701 seeds/m^2) areas ($P=0.0020$)(70% depletion rate). Seed bank species richness per 483cm^2 soil sample was significantly lower where burned (3 species) than unburned (6 species) ($P<0.0001$).

Above-ground herbaceous plants

Total herbaceous plant density was significantly lower in burned (107 plants/m^2) than unburned (329 plants/m^2) areas ($P<0.0001$)(Fig. 2). Non-native density was lower in burned (62 plants/m^2) than unburned (156 plants/m^2) areas ($P<0.0001$). Similarly, native density was lower where burned (45 plants/m^2) than unburned (174 plants/m^2) ($P<0.0001$). Thus, plant densities were reduced 67% during the first postfire spring, and these reductions were similar for native and non-native species. Species richness of herbaceous plants was also significantly lower in burned than unburned areas at 1m^2 (7 species vs. 10 species), 10m^2 (14 vs. 16), 100m^2 (27 vs. 30), and 1,000m^2 (40 vs. 45) spatial scales.

SUMMARY AND CONCLUSIONS

These first year results indicate that the Hackberry Fire Complex of June 2005 had the immediate effects of reducing soil seed bank and herbaceous plant density and diversity during the first postfire fall (October 2005) and spring (April-May 2006) respectively. Typical postfire seeding rates for the Mojave Desert would not have resulted in appreciable increases in seed bank densities if they had been applied after this fire, although our data do not allow us to that these differences would have not have been ecologically significant. The broader implications of these results will be better known after we evaluate results from postfire years 2 and 3.

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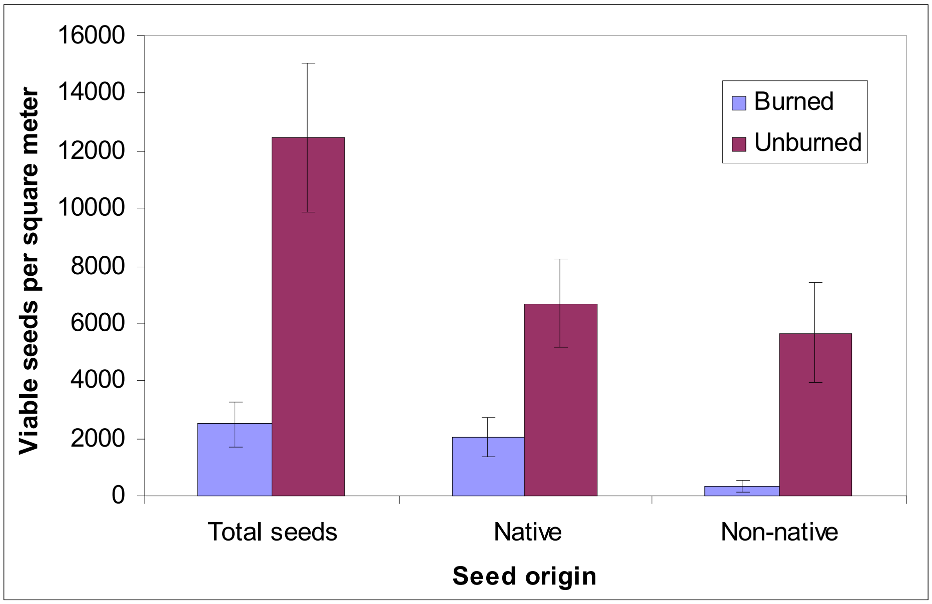

Fig. 1. Density of viable seeds in the seed bank during October 2005 following the June 2005 Hackberry Fire Complex (+/-1 SE, n=6).

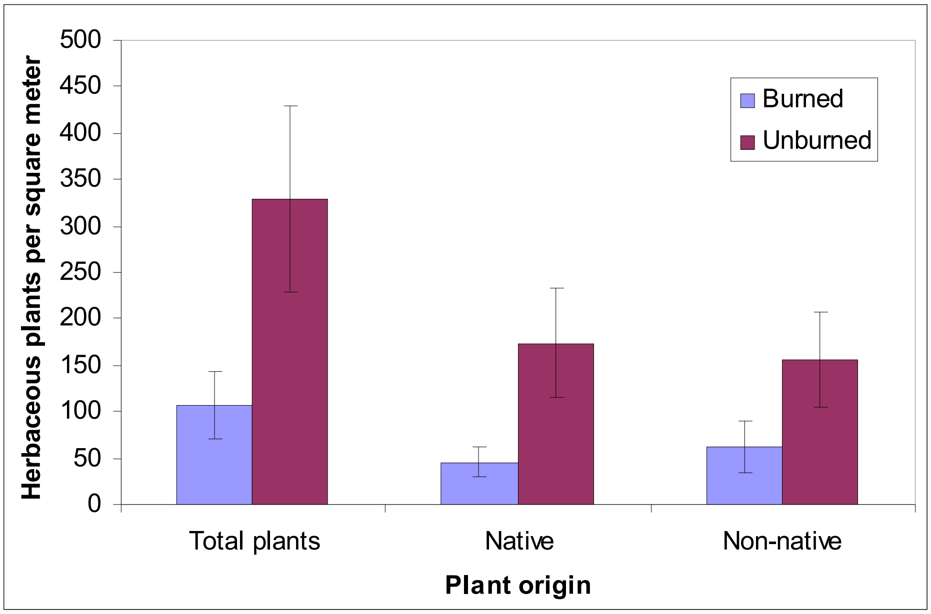

Fig. 2. Herbaceous plant density during April-May 2006 following the June 2005 Hackberry Fire Complex (+/-1SE, n=6).

Am. Midl. Nat. 144:92–108

Competition Between Alien Annual Grasses and Native Annual Plants in the Mojave Desert

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ABSTRACT.—Alien annual grasses in the genera *Bromus* and *Schismus* are widespread and abundant in the Mojave Desert, and negative correlations between these aliens and native annual plants suggest that competition may occur between them. Effects of competition were evaluated by thinning alien annual grass seedlings and measuring the responses of native annual plants at three sites in the central, southcentral and southwestern Mojave Desert during 2 y of contrasting plant productivity. Effects of *Bromus* and *Schismus* were evaluated separately in the microhabitat where each was most abundant, beneath the north side of creosote bushes (*Larrea tridentata*) for *Bromus* and in the open interspace between shrubs for *Schismus*. Thinning of *Bromus* and *Schismus* significantly increased density and biomass of native annuals at all three sites, only during a year of high annual plant productivity and species richness. Effects of thinning were greatest for *Amsinckia tesselata* and for a group of relatively uncommon native annuals. Thinning also significantly increased the density and biomass of the alien forb, *Erodium cicutarium*. These results show that alien annual grasses can compete with native annual plants and an alien forb in the Mojave Desert and that effects can vary among years.

INTRODUCTION

Alien plants can alter the structure of native plant communities. In the Mojave Desert, biomass of alien annual plants is negatively correlated with biomass and species richness of native annuals, even when potential covarying factors such as disturbance and soil nutrient levels are accounted for (Brooks, 1998). In particular, biomass of alien annual grasses is negatively correlated with that of native annuals. These observations suggest that alien annuals may affect the community structure of natives in this region, possibly through interspecific competition.

Two of the most widespread and abundant alien annual plant taxa in the Mojave Desert are the annual grasses *Bromus madritensis* ssp. *rubens* (hereafter called *Bromus rubens*) and *Schismus* spp. (Brooks, 1998; Kemp and Brooks, 1998; Brooks and Berry 1999). These alien grasses affect native desert annuals by promoting wildfires (Brooks, 1999a) and possibly by competing with them for limiting resources such as nitrogen (Brooks, 1998) and water (Eissenstat and Caldwell, 1988; Melgoza and Nowak, 1991). *Bromus rubens* is invasive in its Mediterranean home range and is considered a wildland weed in the Mojave Desert (Brooks, 2000a). It has been present in this region since the early 1900s, but appears to have significantly increased in dominance since the 1970s (Hunter, 1991). *Schismus* spp. (*Schismus arabicus* and *Schismus barbatus*) is not invasive in its Middle Eastern home range, but is considered a wildland weed in the Mojave Desert (Brooks, 2000b). *Schismus* spp. invaded this region during the 1940s and apparently became dominant by the 1950s (O.

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Clarke, pers. comm.). Two other alien annual grasses, *Bromus tectorum* and *Bromus trinii,* are locally abundant but not as widespread and common as *Bromus rubens* and *Schismus* spp. (Brooks, 1998; Kemp and Brooks, 1998; Brooks and Berry 1999).

Although competition has been shown to occur among native desert annuals (Went, 1949; Klikoff, 1966; Inouye *et al.*, 1980; Kadmon and Shmida, 1990; Pantastico-Caldas and Venable, 1993; Venable *et al.,* 1993), it has rarely been demonstrated between native and alien species (Sonoran Desert: Inouye *et al.*, 1980; Pake, 1993; Mojave Desert: Hunter, 1995). Competition between *Bromus rubens* and native annual plants was evaluated in the northern Mojave Desert by experimentally reducing its dominance by thinning and by applying a grass specific herbicide (Hunter, 1995). Although these treatments increased the average density, biomass and species richness of native annual plants, the results were not statistically significant, possibly because of insufficient sample sizes. Competition between *Schismus* and native annuals was reported in the Sonoran Desert where fecundity of *Schismus barbatus* was compared with fecundity of the native annuals *Plantago patagonica* and *Pectocarya recurvata* (Pake, 1993). At high levels of annual plant productivity, fecundity of *Schismus barbatus* was significantly higher than that of the native species, but results varied among productivity levels suggesting that the competitive hierarchies were variable. The competitive effects that dominant alien plants have on natives and the conditions where competition is most likely to occur need to be understood to effectively conserve and restore native plant communities.

The purpose of this study was to test the hypothesis that alien annual grasses in the genera *Bromus* and *Schismus* compete with native annual plants in the Mojave Desert. Competitive effects can be caused by a variety of mechanisms, including interference competition, exploitation competition, apparent competition and higher order interactions (Goldberg and Scheiner, 1993). The common characteristic of these mechanisms is that absolute abundances of plants are higher when and where abundances of their competitors are reduced. The net effect of all possible types of competition is documented in this study.

Competitive effects of alien annual grasses on native annual plants were evaluated by comparing plots that were thinned of alien grasses to unthinned reference plots. Effects were evaluated among three sites and between 2 y to evaluate spatial and temporal variation in competition. The competitive effects of *Bromus* and *Schismus* were evaluated in separate experiments because effects of aliens often vary among taxa (Lodge, 1993).

METHODS

Study sites.—Three individual 1 ha study sites were established in the central, southcentral and southwestern Mojave Desert (Rowlands *et al.*, 1982). The site within each region was located at least 25 m from dirt roads, 1 km from paved roads, 2 km from human habitations, on undeveloped land managed by the United States Department of the Interior, Bureau of Land Management. All sites had granitic soils from the early to middle Holocene which are typical of these regions of the Mojave Desert. Soils at the southwestern site were well drained, gravely, Randsburg sandy loams less than 30 cm deep over a granitic pediment (Valverde and Hill, 1981). Soil surveys were not available for the other two sites, but soils were of similar granitic sandy loam. Longterm rainfall patterns at each site were estimated by averaging the distance-weighted, monthly precipitation averages from the three closest National Oceanic and Atmospheric Administration weather stations (U.S. National Oceanographic and Atmospheric Association, 1995). Winter rainfall amounts were recorded every two weeks from October through April during this study using a single rain gauge at the center of each site.

All sites contained creosote bush scrub plant communities (Munz, 1968) dominated by winter annual plants. Winter annuals germinate from September through December and remain as small vegetative tufts or rosettes until March or April when they rapidly grow, reproduce and die by May (Mulroy and Rundel, 1977). There are over 100 species of winter annuals compared to approximately 15 species of summer annuals in the Mojave Desert (Rowlands *et al.,* 1982). The dominant alien plants at all three sites were the winter annual grasses *Bromus rubens* and *Schismus* spp. and the forb *Erodium cicutarium.* The native winter annual grasses *Vulpia microstachys* and *Vulpia octoflora* were present at all sites, but were uncommon. Plant nomenclature followed Hickman (1993).

The central Mojave site was located south of Black and Opal mountains near Water Valley, San Bernardino County, California (35°07′30″N, 117°07′45″W) at 800 m elevation on a south facing alluvial bajada with 0–3% slope. Long-term average winter rainfall was 79 mm. The perennial plant community was dominated by *Larrea tridentata* and *Ambrosia dumosa,* but also included *Pleuraphis rigida* and *Achnatherum hymenoides.* No livestock grazing was permitted at this site since 1994 (U.S. Fish and Wildlife Service, 1994) and off highway vehicle (OHV) use was limited to roads and a few trails since 1980 (U.S. Bureau of Land Management, 1980a, b).

The southcentral Mojave site was located at the northern edge of the Ord Mountains, San Bernardino County, California (34°41′30″N, 117°57′30″W) at 1100 m elevation on a northwest facing alluvial bajada with 0–5% slope. Longterm average winter rainfall was 78 mm. *Larrea tridentata* and *Ambrosia dumosa* dominated the perennial plant community. No livestock grazing was permitted at this site since 1994 (U.S. Fish and Wildlife Service, 1994) and OHV use was limited to roads and a few trails since 1980 (U.S. Bureau of Land Management, 1980a, b).

The southwestern Mojave site was located at the southwest tip of the Rand Mountains in the Desert Tortoise Research Natural Area, Kern County, California (35°14′30″N, 117°51′15″W) at 870 m elevation on a southwest facing alluvial bajada with 0–5% slope. Longterm average winter rainfall was 104 mm. *Larrea tridentata* and *Ambrosia dumosa* dominated the perennial plant community. This site was closed to OHV use in 1973 and livestock grazing in 1976 (U.S. Bureau of Land Management, 1980ab). Further descriptions of the southwestern Mojave site can be found in Brooks (1999b).

Thinning treatments.—Effects of competition were tested by thinning the seedlings of two dominant alien annual grass genera, *Bromus* and *Schismus,* at the beginning of the growing season and evaluating the effects of thinning on density and biomass of native annuals at the end of the growing season. The relative composition of *Bromus* seedlings that were thinned was estimated because the individual species were difficult to distinguish as seedlings. *Bromus* seedlings were composed of approximately 90% *Bromus rubens* and 10% *Bromus tectorum* and *Bromus trinii.* The relative composition of *Schismus* seedlings that were thinned could not be reliably estimated.

Bromus and *Schismus* seedlings were thinned in the microhabitat where each was most abundant (Samson, 1986; Brooks, 1998; Brooks 1999c) and therefore most likely to compete with natives. *Bromus* seedlings were thinned beneath the canopy on the north side of creosote bushes (*Larrea tridentata*) (beneath-canopy microhabitat). *Schismus* seedlings were thinned in the open space between the canopies of perennial shrubs and bunchgrasses (interspace microhabitat). Seedlings were thinned using forceps and scissors and disposed of away from the plots. All aboveground portions of living plants were removed, leaving the roots intact and the soil undisturbed. Thus, alien annual grass seedlings were not completely removed, but their overall rates of photosynthesis and consumption of nutrients were reduced compared to unthinned reference plots.

Thinning treatments began when seedlings emerged approximately two weeks after the first and only cohort of annual plants germinated during each year. The time that the treatments began varied by two weeks among sites within each year. All treatments began in January, ended in February and consisted of an initial thinning followed by a second thinning two to three weeks later. In 1996, the average number (±1 SE) of *Bromus* seedlings thinned per 500 cm^2 plot was 128 ± 14 and the average number of *Schismus* thinned was 29 ± 4. In 1997, the average number of *Bromus* seedlings thinned per plot was 253 ± 33 and the average number of *Schismus* thinned was 52 ± 12.

Thinning experiments of this type are commonly used to evaluate competition in situ within plant communities, but they have problems (Campbell *et al.,* 1991; Goldberg and Barton, 1992). One problem is that soil disturbance and root death of thinned plants can affect soil microbial processes and the amounts of mineral nutrients such as nitrogen (Wilson and Tilman, 1991; McLennan *et al.*, 1995). Thus, effects of thinning can be erroneously attributed to competitive release when they are actually a result of altered levels of soil nutrients. Another problem is that thinning effects can vary within years depending on the phenological stages of plant species when thinning is applied (Campbell *et al.*, 1991), and possibly among years depending on the productivity and species composition of annual plant seedlings. These potential confounding effects were evaluated in the current study by monitoring levels of nitrate and ammonium in the soil of thinned and reference plots, thinning during years when only one cohort of seedlings emerged, and documenting community biomass and species composition during each year.

Experimental and sampling design.—Experimental factors were replicated at 25 stations arranged in a 5 × 5 grid at 25 m intervals within each of the three study sites. At each station four contiguous 20 × 25 cm (500 cm^2) experimental plots were placed end-to-end on their long axes in each of two microhabitats. For the *Bromus* thinning experiment, the experimental plots were placed in the beneath-canopy microhabitat of the closest creosote bush located in a random compass direction from each station. The four plots were oriented in an arc (~30°) corresponding to the position of the beneath-canopy microhabitat. Beneath-canopy microhabitats were only used for creosote bushes with canopy diameters of at least 150 cm so the four experimental plots would fit completely within this microhabitat. For the *Schismus* thinning experiments, the experimental plots were placed in the closest interspace microhabitat located in a random compass direction >1 m from the creosote bush used for the beneath-canopy microhabitat at each station. The four plots were placed end to end in an arc of the same shape as described above for the beneath-canopy microhabitat. Individual experimental plots were randomly assigned a single level of each experimental factor, treatment (thinning and reference) and year (1996 and 1997). Hence, two plots served as thinning and reference plots during 1996 and two others served as thinning and reference plots during 1997. The total number of treatment plots was 600 (2 years × 2 treatments × 2 species(microhabitats) × 25 stations × 3 sites).

The responses of native annual plants to the thinning treatments were evaluated by collecting annual plant samples when winter annuals reached peak biomass and before they began to senesce. Samples were collected 10–18 April 1996 and 9–17 March 1997. Live annual plants were clipped at ground level within 10 x 20 cm sampling frames, counted by species, dried to a constant mass at 60 C and weighed to determine aboveground live dry biomass. Each sampling frame was centered within the 500 cm^2 experimental plots. Samples from the 2 y were considered repeated measures, because they were collected within 1 m of each other from the same microhabitat located within each station at each site.

Soil samples were collected from a random subset of six sampling frames in each of the two microhabitats after annual plants were harvested in March 1997. Samples were 8 cm diameter by 7 cm deep and were centered within the sampling frame. Soils were immedi-

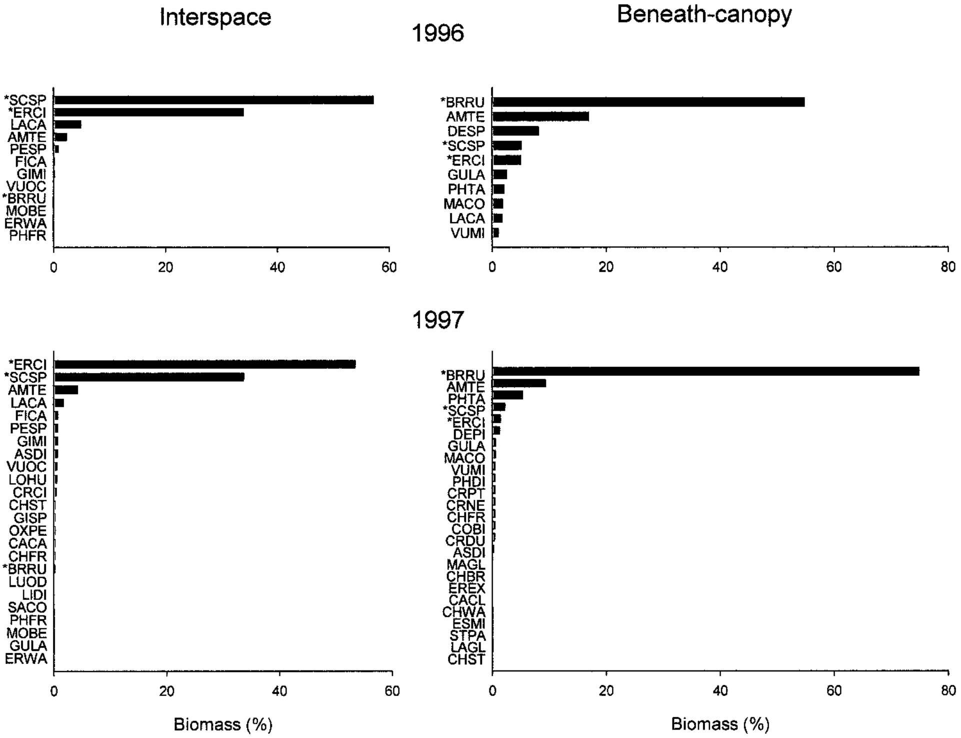

FIG. 1.—Percent biomass of annual plant species in interspace and beneath canopy microhabitats in 1996 and 1997. Species codes are defined in Appendix A; * = alien species

ately sieved (2 mm), stored in airtight plastic bags and analyzed by the University of California, Davis, Division of Agricultural and Natural Resources Analytical Laboratory.

Analysis of data.—Five dominant native annual plant taxa were evaluated individually, and the remaining less dominant native annuals were evaluated collectively as a group called "other natives" (n = 6 response variables). The dominant taxa had the highest density and biomass among natives within each microhabitat during both years at all sites, although their order of dominance varied between years (Fig. 1). The composition of the other natives group varied between microhabitats and between years. For the *Bromus* experiment, the response variables included *Amsinckia tesselata, Descurania pinnata, Malacothrix coulteri, Gullenia lasiophyllum, Phacelia tanacetifolia* and other natives. For the *Schismus* experiment, the response variables included *Amsinckia tesselata, Filago californica, Gilia minor, Lasthenia californica, Pectocarya* spp. and other natives.

Treatment effects were evaluated separately for *Bromus* thinning in the beneath-canopy microhabitat and *Schismus* thinning in the interspace microhabitat. All treatment-by-site, treatment-by-sampling station and treatment-by-site-by-sampling station interactions were not significant ($P > 0.250$), so these terms were pooled in the final model (3 sites × 25 sampling stations = 75 spatial replicates) (Underwood, 1997). The final general linear model was balanced with two fixed factors, treatment nested within year. Data were transformed using square root $(x + 0.5)$ for density and species richness and $\log_{10}(x + 1)$ for biomass (Sokal and Rohlf, 1995). These transformations made the data more normally distributed and homoscedastic.

The data were analyzed in four steps. First, graphical plots were created displaying the average density and biomass of the dominant native and alien annual plant taxa in thinning and reference treatments during 1996 and 1997. Dominant alien plants were included to evaluate the effects of thinning on the alien grass taxa that were thinned, and to evaluate potential indirect effects of thinning on natives that may have been mediated through alien taxa that were not thinned (*e.g., Erodium cicutarium*). Second, repeated measures analysis of variance (ANOVA) was used to evaluate the significance of thinning treatments on total density and biomass of all native annual plants combined during each of the two years ($\alpha \leq 0.050$). Expected mean squares and significance tests were calculated using the GLM procedure and REPEATED statement of SAS statistical software (SAS Institute, 1985). Third, multivariate analysis of variance (MANOVA) was used to evaluate the significance of thinning treatments within each year on the density and biomass of five dominant, native, annual plant taxa plus the other natives group (6 response variables). MANOVA was used instead of multiple univariate ANOVAs because it does not require equal correlations among the response variables, it reduces the chance of type I errors that can occur with multiple univariate analyses, and it allows analyses of relationships among response variables (Scheiner, 1993; von Ende, 1993). Hotelling T^2 statistic was used to evaluate multivariate differences between thinning and reference plots (Morrison 1967). Degrees of freedom for the F-value of each MANOVA were p and $(N_1 + N_2 + p - 1)$, where $p = 6$ (response variables) and $N_1 = N_2 = 75$ (replicates). Standardized canonical coefficients and graphical plots were used to evalute the relative effect of thinning treatments on each response variable. Expected mean squares, significance tests, and standardized canonical coefficients were calculated using the GLM procedure and the MANOVA statement with the CANONICAL option (SAS, 1988). This procedure produced values of Wilks' λ, from which the Hotelling T^2 statistic was calculated using the formula: $T^2 = (n - 1)\ (1 - \lambda/\lambda)$ (Khattree and Naik 1995). Fourth, the significance of the six response variables used in each MANOVA were evaluated individually using ANOVA and bonferroni corrected type I error rates ($P \leq 0.05/6$ tests $= 0.0083$) (Sokal and Rohlf, 1995).

RESULTS

The amount and temporal distribution of winter (Oct.–Apr.) rainfall was similar at the three study sites, but differed between years during this study. In 1995–1996, winter rainfall averaged 94% of average (82 mm) and occurred in small increments throughout the winter. In 1996–1997 rainfall averaged 77% of average (67 mm), but occurred mostly in December when rainfall was 307% of average for that month (46 mm). This high December rainfall stimulated mass germination of annual plants which resulted in high biomass and species richness of annual plants during spring 1997. In the interspace microhabitat, amounts were higher in 1997 than 1996 for average (±1 SE) annual biomass (1.05 ± 0.11 vs. 0.32 ± 0.15 g/200 cm^2) and species richness (6.78 ± 0.32 vs. 1.77 ±0.10 species/200 cm^2). In the beneath-canopy microhabitat, amounts were also higher during 1997 than 1996 for average annual plant biomass (4.21 ± 0.40 vs. 0.12 ± 0.02 g/200 cm^2) and species richness (8.06 ± 0.35 vs. 1.79 ± 0.08 species/200 cm^2). Species composition also differed between years, with many more native species present in 1997 than 1996 (Fig. 1). Forty three species of annual plants were collected in this study (Appendix A), three of which were aliens which composed the majority of the total community biomass (Fig. 1).

Thinning treatments did not affect the amount of nitrate or ammonium present in the soil at the time annual plants were collected on 9–17 March 1997. In the beneath-canopy

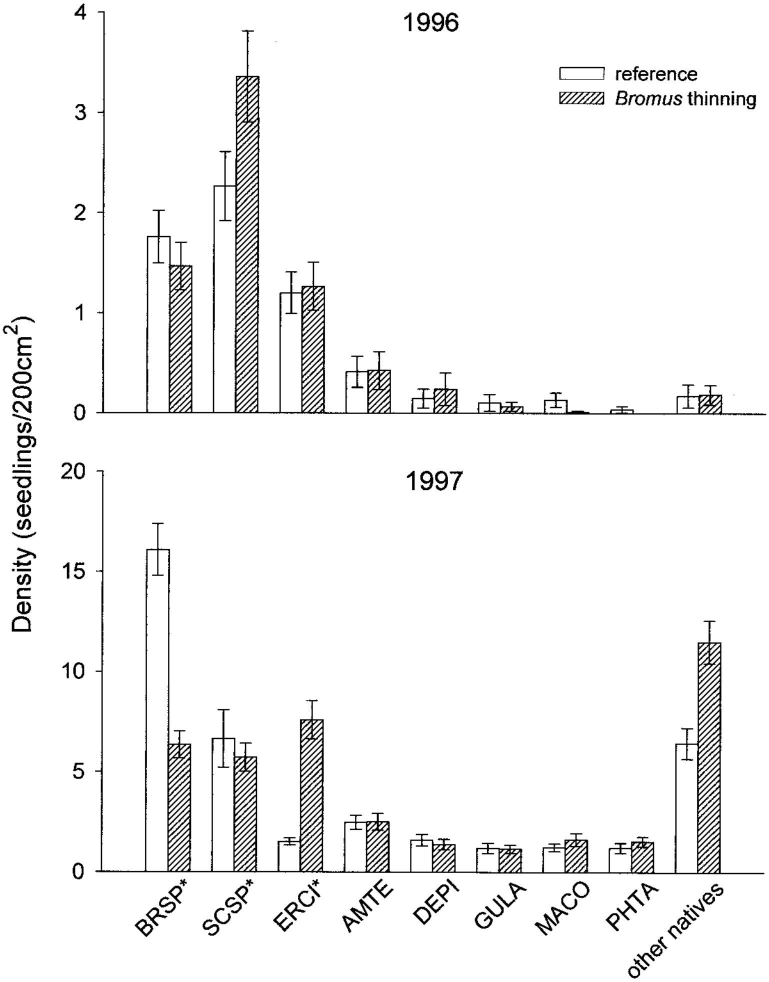

FIG. 2.—Effects of *Bromus* thinning on the density of annual plants in the beneath canopy microhabitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Descurania pinnata, Guillenia lasiophylla, Malacothrix coulteri, Phacelia tanacetifolia* and other native annuals. Species codes are defined in Appendix A; * = alien species

microhabitat, average (±1 SE) nitrate levels were 10.1 ± 1.1 ppm in treatment plots and 11.2 ± 0.9 ppm in reference plots, and ammonium levels were 3.4 ± 0.8 ppm in treatment plots and 3.7 ± 0.7 ppm in reference plots. In the interspace microhabitat, average nitrate levels were 4.8 ± 0.3 ppm in treatment plots and 4.9 ± 0.2 ppm in reference plots and ammonium levels were 1.1 ± 0.1 ppm in treatment plots and 1.0 ± 0.2 ppm in reference plots.

Effects of Bromus thinning.—Thinning reduced, but did not completely remove, density and biomass of *Bromus* in treatment compared to reference plots (Figs. 2, 3). In 1996 *Bromus* density was 17% and biomass was 4% lower in treatment than reference plots. In

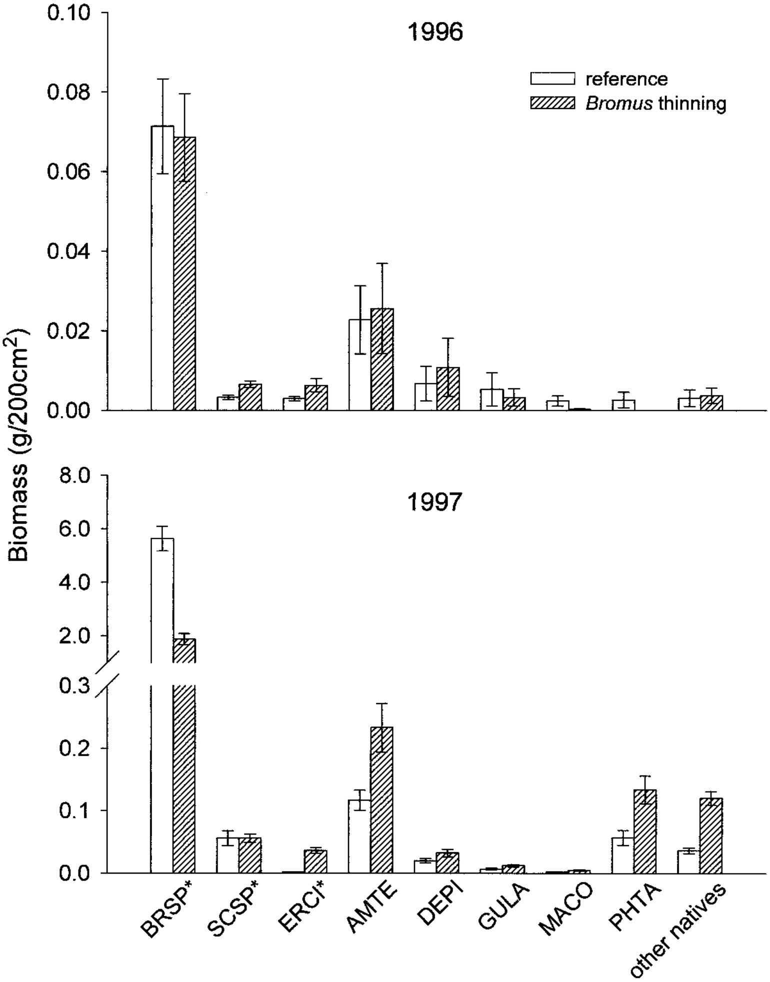

FIG. 3.—Effects of *Bromus* thinning on the biomass of annual plants in the beneath canopy microhabitat. Values represent the average of 25 replicates at three study sites ($n = 75$, $+1$ SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Descurania pinnata, Guillenia lasiophylla, Malacothrix coulteri, Phacelia tanacetifolia* and other native annuals. Species codes are defined in appendix A; * = alien species

1997, *Bromus* density was 61% and biomass was 67% lower in treatment than reference plots.

Thinning *Bromus* seedlings significantly affected the total density ($F_{1,148} = 8.53$, $P = 0.004$) and biomass ($F_{1,148} = 22.57$, $P < 0.001$) of native annual plants. Effects of thinning differed significantly between years, as indicated by significant treatment-by-year interactions for density ($F_{1,148} = 12.25$, $P = 0.001$), and biomass ($F_{1,148} = 35.15$, $P < 0.001$). Density and biomass of native annuals was significantly affected by thinning *Bromus* in 1997 ($F_{1,148} = 10.89$, $P = 0.001$ and $F_{1,148} = 32.58$, $P < 0.001$ respectively), but not in 1996 ($F_{1,148} = 0.03$, $P = 0.865$ and $F_{1,148} = 0.01$, $P = 0.980$ respectively). Density of natives (seedlings/

TABLE 1.—MANOVA of the effects of *Bromus* thinning in the beneath-canopy microhabitat on the density and biomass of *Amsinckia tesselata, Filago californica, Gilia minor, Lasthenia californica, Pectocarya* spp. and other native annuals

Response variable	Hotelling's T^2	F	df	P
1996				
Density	6.19	1.02	6, 143	0.412
Biomass	6.14	1.03	6, 143	0.407
1997				
Density	14.53	2.58	6, 143	0.021
Biomass	46.75	10.90	6, 143	<0.001

200 cm² ±1 SE) was 19.61 ± 1.43 on *Bromus*-thinned plots compared to 14.21 ± 0.88 on reference plots in 1997, and 0.93 ± 0.36 on thinned plots compared to 1.01 ± 0.29 on reference plots in 1996. Biomass of natives (g/200 cm²) was 0.06 ± 0.02 on thinned plots compared to 0.05 ± 0.02 on reference plots in 1997, and 0.54 ± 0.06 on thinned plots compared to 0.24 ± 0.03 on references plots in 1996.

The multivariate effect of *Bromus* thinning on the six dominant native taxa was significant in 1997 but not 1996 (Table 1), although not all individual taxa were affected equally (Figs. 2, 3). For density, standardized canonical coefficients indicated that the other natives category was the group most affected by thinning treatments in 1997 (Table 2; $F_{1,148} = 14.50$, $P < 0.001$). For biomass, other natives ($F_{1,148} = 48.49$, $P < 0.001$) and *Amsinckia tesselata* ($F_{1,148} = 7.63$, $P < 0.001$) were most affected by treatments.

Bromus thinning did not significantly reduce the density or biomass of *Schismus,* but did significantly reduce density and biomass of a third dominant alien, *Erodium cicutarium,* during 1997 (Figs. 2, 3). Density of *Erodium cicutarium* was significantly higher on thinned than reference plots in 1997 ($F_{1,148} = 39.50$, $P < 0.001$) but not 1996 ($F_{1,148} = 0.40$, $P = 0.884$), and biomass of *Erodium cicutarium* was significantly higher on thinned plots during 1997 ($F_{1,148} = 57.11$, $P < 0.001$) but not 1996 ($F_{1,148} = 3.76$, $P = 0.054$).

Effects of Schismus thinning.—Thinning reduced, but did not completely remove, density and biomass of *Schismus* in treatment compared to reference plots (Figs. 4, 5). In 1996, *Schismus* density was 81% and biomass was 65% lower in treatment than reference plots. In 1997, *Schismus* density was 90% and biomass was 83% lower in treatment than reference plots.

Thinning *Schismus* seedlings significantly affected the total density ($F_{1,148} = 14.73$, $P < 0.001$) and biomass ($F_{1,148} = 8.86$, $P = 0.003$) of native annual plants. Effects of thinning differed significantly between years, as indicated by significant treatment-by-year interactions

TABLE 2.—Standardized canonical coefficients of the first eigenvalue for the MANOVA of *Bromus* thinning in the beneath-canopy microhabitat on the density and biomass of native annual plant taxa during spring 1997. The magnitude of each coefficient corresponds to the relative effect of thinning on each response variable. Species codes are defined in appendix A

	AMTE	DEPI	GULA	MACO	PHTA	Other natives
Density	0.205	−0.202	−0.160	0.150	0.039	1.004
Biomass	0.462	0.072	0.217	0.263	0.173	0.850

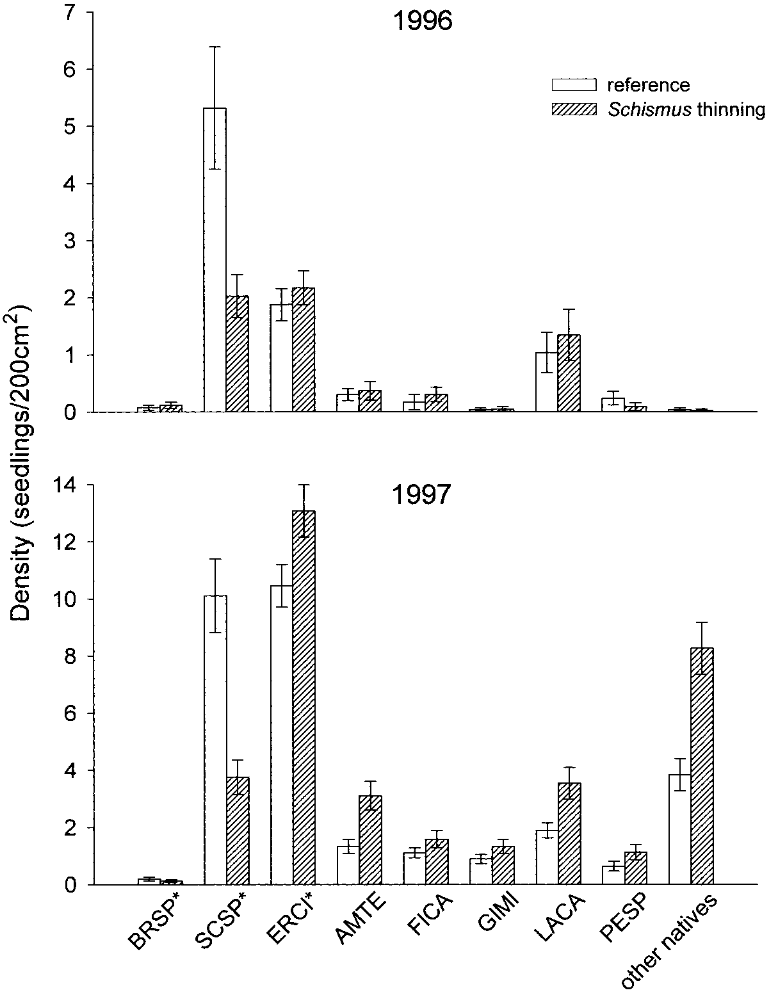

FIG. 4.—Effects of *Schismus* thinning on the density of annual plants in the beneath canopy microhabitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Amsinckia tesselata, Filago californica, Lasthenia californica, Pectocarya* spp. and other native annuals. Species codes are defined in Appendix A; * = alien species

for density ($F_{1,148} = 17.41$, $P < 0.001$), and biomass ($F_{1,148} = 15.42$, $P < 0.001$). Density and biomass of native annuals were significantly affected by thinning in 1997 ($F_{1,148} = 23.24$, $P < 0.001$ and $F_{1,148} = 14.05$, $P < 0.001$), but not in 1996 ($F_{1,148} = 0.07$, $P = 0.793$ and $F_{1,148} = 0.64$, $P = 0.426$). Density of natives (seedlings/200 cm^2) was 19.43 ± 1.40 on *Schismus*-thinned plots compared to 9.89 ± 0.75 on reference plots in 1997 and 2.12 ± 0.50 on thinned plots compared to 1.84 ± 0.40 on references plots in 1996. Biomass of natives (g/200 cm^2) was 0.18 ± 0.2 on thinned plots compared to 0.08 ± 0.01 on reference plots in 1997, and 0.03 ± 0.01 on thinned plots compared to 0.03 ± 0.01 on references plots in 1996.

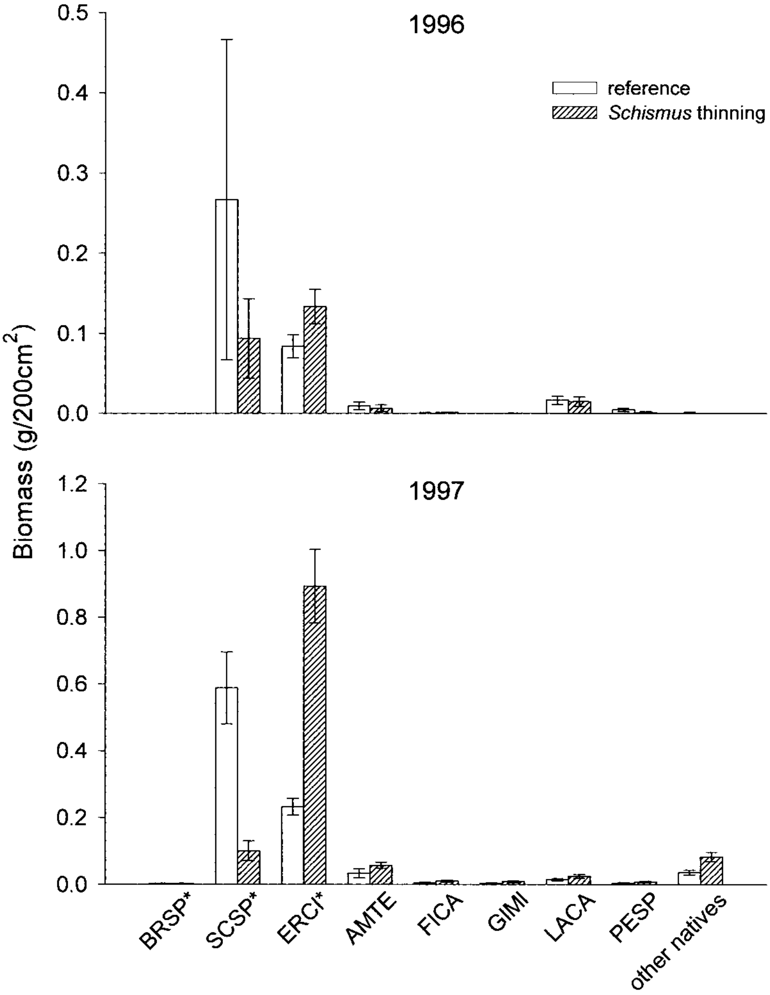

FIG. 5.—Effects of *Schismus* thinning on the biomass of annual plants in the beneath canopy microhabitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Amsinckia tesselata, Filago californica, Lasthenia californica, Pectocarya* spp. and other native annuals. Species codes are defined in Appendix A; * = alien species

The multivariate effect of *Schismus* thinning on dominant native taxa was also significant in 1997 but not 1996 (Table 3), although not all individual taxa were affected the same (Figs. 4, 5). Standardized canonical coefficients of density indicated that *Amsinckia tesselata* ($F_{1,148}$ = 7.45, P = 0.007) and other natives ($F_{1,148}$ = 12.63, P = 0.001) were the native taxa most affected by thinning treatments in 1997 (Table 4). Biomass of other natives was most affected by treatments in 1997 ($F_{1,148}$ = 9.63, P = 0.002).

Schismus thinning did not significantly affect density or biomass of *Bromus* because *Bromus* was uncommon in the interspace microhabitat (Figs. 4, 5). After *Schismus* thinning, *Erodium cicutarium* significantly increased in density during 1997 ($F_{1,148}$ = 4.98, P = 0.027)

TABLE 3.—MANOVA of the effects of *Schismus* thinning in the interspace microhabitat on the density and biomass of *Amsinckia tesselata, Descurania pinnata, Guillenia lasiophylla, Malacothrix coulteri, Phacelia tanacetifolia* and other native annuals

Response variable	Hotelling's T^2	F	df	P
1996				
Density	2.80	0.46	6, 143	0.840
Biomass	4.85	0.86	6, 143	0.570
1997				
Density	20.34	3.77	6, 143	<0.001
Biomass	14.50	2.57	6, 143	<0.001

but not 1996 ($F_{1,148} = 0.53$, $P = 0.469$), and in biomass during 1997 ($F_{1,148} = 39.99$, $P < 0.001$) but not 1996 ($F_{1,148} = 3.38$, $P = 0.068$).

Other observations.—Native annual plant seedlings in reference plots began to senesce approximately 2 wk earlier than those in thinned plots during 1997. Withering shoot tissue marked the onset of senescence. Many of these senescent seedlings died before they produced seeds and were not included in the samples of live annual plants collected in March 1997. The differential senescence of annual plants between treatments was not observed in 1996.

DISCUSSION

The results of this study support the hypothesis that competition occurs between alien annual grasses and native annual plants in the Mojave Desert. Thinning of alien annual grasses increased total density and biomass of native annual plants, but significantly affected only one of the five most dominant native species. This species, *Amsinckia tesselata,* is a common forb in disturbed areas of the Mojave Desert (Hickman, 1993). The results of this study should be interpreted cautiously because it was designed to evaluate the net effects of competition. Possible indirect effects between and among alien and native species prevent definitive conclusions regarding the mechanisms of competition. Evidence is discussed below that implicates certain mechanisms that are proposed as hypotheses for further study.

Thinning treatments can produce unwanted effects that complicate the interpretation of plant competition experiments (Campbell *et al.*, 1991; Goldberg and Barton, 1992), but these confounding effects were not detected in the current study. For example, thinning treatments did not affect levels of available nitrogen in the soil, indicating that thinning did not cause changes in soil fertility. In addition, the soil was left undisturbed on thinned plots, so surface disturbance was not a factor causing differences between treatment and

TABLE 4.—Standardized canonical coefficients of the first eigenvalue for the MANOVA of *Schismus* thinning in the interspace microhabitat on the density and biomass of native annual plants during spring 1997. The magnitude of each coefficient corresponds to the relative effect of thinning on each response variable. Species codes are defined in appendix A

	AMTE	FICA	GIMI	LACA	PESP	Other natives
Density	0.619	0.058	0.256	0.280	0.129	0.612
Biomass	0.470	0.312	0.239	0.140	0.061	0.633

reference plots. Alien annual grasses can also affect natives by altering fire regimes, biogeochemical cycles and rates of leaf litter accumulation (D'Antonio and Vitousek, 1992), but these effects should not occur within the four month interval of this experiment during each year. Thus, it seems reasonable to conclude that the effects of thinning were attributable to reduced net competition from alien annual grasses.

The mechanisms by which annual plants compete with each other result in different outcomes with respect to density and biomass. Densities of annual plants can either be affected by germination inhibition or by post-germination competition for limiting resources in the deserts of southwestern North America (Went, 1949; Juhren *et al.*, 1956; Inouye, 1980; Inouye *et al.*, 1980). In contrast, biomass of annual plants is affected primarily by post-germination competition (Inouye, 1991). In the current study there was only one cohort of annual plants that germinated each year and thinning treatments were applied after these seedlings germinated, so the effects of thinning should have been caused by post-germination competition.

Accelerated senescence of native annual plants in thinned compared to reference plots suggest that alien annual grasses competed with native seedlings for water and mineral nutrients as these nutrients became less abundant at the end of the growing season. *Bromus rubens, Schismus* spp. and *Erodium cicutarium* can assimilate nitrogen faster than native annuals in the central, southern and western Mojave Desert (Brooks, 1998), and *Bromus tectorum* can acquire water more rapidly than native annuals in the Great Basin desert (Eissenstat and Caldwell, 1988; Melgoza and Nowak, 1991). Nitrogen and water are considered to be the two primary factors that limit plant growth in the Mojave Desert (Rundel and Gibson, 1996). Hence, the competitive superiority of some alien annuals may be linked to competition for these nutrients. Experimental manipulations of seedling densities and nutrient levels are required to test this hypothesis.

Effects of thinning were similar at all three study sites and significant only during a year of overall high productivity, suggesting that competition of aliens with natives may be widespread but varies among years. However, these hypotheses require additional testing because site and year were fixed effects in this study. Moreover, the sites were all in plant communities dominated by the widespread and common perennial shrub *Larrea tridentata,* and interactions between alien and native annuals may be different in other plant communities. In addition, the 2 yr studied differed in biomass, species richness and species composition of annual plants, all factors that may affect competitive hierarchies. Studies documenting the net effects of competition should not be generalized beyond their spatial and temporal ranges, because the multiple mechanisms that influence these net effects can vary in space and time (Goldberg and Scheiner, 1993).

Thinning treatments increased the density and biomass of *Erodium cicutarium,* a widespread and abundant alien annual forb. This species has been present in southwestern North America since the 1600s (Mensing and Byrne, 1999), in contrast to most other exotic annuals that invaded during the late 1800s and early 1900s (Heady, 1988). The increase in density and biomass of *E. cicutarium* was approximately equal to the reduction of alien annual grass abundance on thinned plots, resulting in no net change in the proportional density and biomass of aliens (Brooks, 1998). Because the density and biomass of native annual plants increased despite similar increases in *E. cicutarium,* competition between them does not appear to have been significant. However, other evidence suggests *E. cicutarium* may compete with native annuals, based on negative correlations between their abundances in the Mojave (Brooks, 1998) and Sonoran Deserts (Inouye *et al.*, 1980). Tests of the relationships between *E. cicutarium* and native annuals are required to draw any reliable conclusions about their competitive relationships.

Bromus and *Schismus* may compete with different subsets of the native annual plant community, based on their respective dominance of the beneath-canopy and interspace microhabitats and because thinning of these taxa in the microhabitat where they were each uncommon did not affect native annual plants (Brooks, 1998). Because many native annuals display preferences for one or the other of these microhabitats (Shreve, 1931; Went, 1942; Muller, 1953; Halvorson and Patten,1975; Shmida and Whittaker, 1981), *Bromus* and *Schismus* may compete with different suites of annual plant species. However, there are areas in the Mojave Desert where *Bromus* density and biomass is high across the landscape in both microhabitats (Brooks, 1998), and in these areas *Bromus* may compete with a wider range of annual plants than was observed in the current study.

The composition of annual plant communities in the Mojave Desert can vary greatly among seasons and germination cohorts (Jennings, 1993; Burk, 1982), and the results of the current study may have differed given a different suite of annual plant seedlings. This study focused on winter-germinating annual plants that grew together in a single germination cohort during each of two years. It is unknown if the effects of thinning would have been different had a second cohort of annual plants germinated after the thinning treatments were applied each year. It is also unknown if these alien winter annuals compete with native summer annuals that grow from late winter through early summer. If alien winter annuals use large amounts of soil nutrients during winter and spring, then they may affect summer annuals by reducing the amounts of nutrients available during spring and summer. This hypothesis requires testing, especially in the eastern part of the Mojave Desert where summer annuals are most abundant (Rowlands *et al.*, 1982).

This study demonstrates that alien annual grasses can significantly affect the density and biomass of native annual plant seedlings. Years of competition from these grasses may reduce the seed banks of native annuals, possibly causing fundamental changes in annual plant community structure and food web dynamics. The results also highlight the need to evaluate the effects of all dominant alien taxa, because aliens such as *Erodium cicutarium* may increase in dominance when alien annual grasses are removed. This conclusion is especially important to keep in mind when implementing management practices designed to minimize the dominance of individual species of alien annual plants.

Acknowledgments.—Funding for this study was provided by the United States Department of the Interior, Interagency Fire Coordination Committee and the United States Geological Survey, Biological Resources Division. I thank Mary Price, Kristin Berry, John Rotenberry, Richard Minnich, Edith Allen, Peter Stine and three anonymous reviewers for their helpful reviews of this manuscript.

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SUBMITTED 5 APRIL 1998 ACCEPTED 17 JANUARY 2000

APPENDIX A.—Annual plants collected April 1996 and March 1997 at the DTNA

Amsinckia tesselata	AMTS	NF[1]	*Gilia minor*	GIMI	NF
Astragalus didymocarpus	ASDI	NF	*Gilia* species	GISP	NF
Bromus rubens	BRRU	AG	*Guillenia lasiophylla*	GULA	NF
Bromus species	BRSP	AG	*Lasthenia californica*	LACA	NF
Bromus tectorum	BRTE	AG	*Layia glandulosa*	LAGL	NF
Bromus trinii	BRTR	AG	*Linanthus dichotomus*	LIDI	NF
Camissonia campestris	CACA	NF	*Lotus humistratus*	LOHU	NF
Camissonia claviformis	CACL	NF	*Lupinus odoratus*	LUOD	NF
Chenactis fremontii	CHFR	NF	*Malacothrix coulteri*	MACO	NF
Chenactis steviodes	CHST	NF	*Malacothrix glabrata*	MAGL	NF
Chorizanthe brevicornu	CHBR	NF	*Monoptillon belliforme*	MOBE	NF
Chorizanthe watsonii	CHWA	NF	*Oxytheca perfoliata*	OXPE	NF
Coreopsis bigelovii	COBI	NF	*Pectocarya* species	PESP	NF
Crypthantha circumcissa	CRCI	NF	*Phacelia distans*	PHDI	NF
Crypthantha dumetorum	CRDU	NF	*Phacelia fremontii*	PHFR	NF
Crypthantha nevadensis	CRNE	NF	*Phacelia tanacetifolia*	PHTA	NF
Crypthantha pterocarya	CRPT	NF	*Salvia columbariae*	SACO	NF
Descurainia pinnata	DEPI	NF	*Schismus* species	SCSP	AG
Eremalche exilis	EREX	NF	*Schismus arabicus*	SCAR	AG
Eriophyllum wallacei	ERWA	NF	*Schismus barbatus*	SCBA	AG
Erodium cicutarium	ERCI	AF	*Stephanomeria parryi*	STPA	NF
Escholtzia minutiflora	ESMI	NF	*Vulpia microstachys*	VUMI	NG
Filago californica	FICA	NF	*Vulpia octoflora*	VUOC	NG

[1] AF = alien forb, AG = alien grass, NF = native forb, NG = native grass

Western North American Naturalist 61(1), © 2001, pp. 25–35

EXPERIMENTAL MANIPULATIONS OF FERTILE ISLANDS AND NURSE PLANT EFFECTS IN THE MOJAVE DESERT, USA

Lawrence R. Walker[1], Daniel B. Thompson[1], and Frederick H. Landau[1]

ABSTRACT.—In a mixed desert shrub community we removed and added shrub canopies to examine above- and belowground influences of 3 species of shrubs on islands of soil fertility and the survival of transplanted *Ambrosia dumosa* seedlings. Soils sampled under shrubs in the wet season had higher pH, water content, organic matter, and both total and mineralizable nitrogen than soils in adjacent open areas, confirming a widely established pattern in arid lands. However, we also found species differences in soil parameters. Soils under *Coleogyne ramosissima* had highest pH, soils under *A. dumosa* had highest water content and nitrogen mineralization rates, and soils under *Larrea tridentata* had lowest water content. Soils sampled under shrubs in the dry season, 7 months after experimental shrub removal, maintained higher organic matter and total and mineralizable nitrogen content than adjacent open soils, but pH and water were altered by shrub manipulations. Species differences persisted only in soil water levels (*A. dumosa* soils were driest). Over a 1-year period, transplanted *A. dumosa* seedlings had highest survivorship in shrub removal and open treatments and died most rapidly under control shrubs of all 3 species, suggesting that shrubs had a strong negative effect on seedling survival, even in the presence of higher organic matter, nutrients, and (initially) higher water content of fertile islands. Our results suggest that nurse plants and islands of soil fertility have the potential to facilitate growth of other species by nutrient additions, but that the net effect of nurse plants can be negative due to shading and/or root competition.

Key words: competition, facilitation, aridland soils, Ambrosia dumosa, Coleogyne ramosissima, Larrea tridentata.

The pattern of higher soil fertility under desert shrubs than in adjacent open areas is well documented for arid lands (Charley and West 1975, Virginia 1986, Franco and Nobel 1989, Garner and Steinberger 1989, Schlesinger et al. 1996). Colonization of open areas (e.g., by species in the genus *Ambrosia*; McAuliffe 1988) apparently begins a cycle of habitat amelioration in deserts in which organic matter is built up from plant litter and entrapment of wind-blown debris, and further enhanced by secondary colonization of other shrubs and annuals. Animals presumably contribute to soil nutrients, and their burrowing under shrubs increases soil aeration and water infiltration to deeper soil layers (Garner and Steinberger 1989). These "fertile islands" under desert shrubs are therefore distinguished from adjacent open areas between shrub canopies by higher levels of organic matter and soil nutrients, higher rates of nutrient turnover, higher soil water content, higher productivity of annual plants, and increased soil microbe and vertebrate animal activity. Although these properties of fertile islands may enhance recruitment of new seedlings under shrubs, shrub roots may also compete with seedlings for available nutrients and water, and canopies of established shrubs may reduce light levels enough to limit primary productivity of understory seedlings (Charley and West 1975, Franco and Nobel 1989, Hunter 1989, Callaway et al. 1996). The net effect of these potentially positive and negative attributes of desert shrubs on recruitment of new seedlings can best be examined with experimental manipulations of fertile islands and associated shrubs.

Fertile islands have important effects on the dynamics of desert ecosystems. Experimental studies of desert ecology have demonstrated that establishment and growth of dominant shrub species are limited by nitrogen and water (Fonteyn and Mahall 1981, Lajtha 1987, Smith et al. 1987, Fisher et al. 1988, Lajtha and Whitford 1989). Thus, it is not surprising that there is strong evidence from arid lands of nurse plants that facilitate establishment of other species (McAuliffe 1984, 1988, Franco and Nobel 1989). As the facilitated plant grows, it may eventually out-compete the nurse plant. The fertile island can thus become the center of a centuries-long process of colonization and

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succession where nutrient cycling, plant productivity, and animal activities are all higher than in intershrub spaces.

In this study we experimentally examined similarities and differences between above- and belowground influences of 3 species of desert shrubs on properties of fertile islands and transplanted seedlings by removing and adding shrub canopies. Species differences in fertile island characteristics were recognized by Charley and West (1975) but rarely have been examined experimentally. We examined the effect of shrub canopy removal treatments on survival of transplanted seedlings of *Ambrosia dumosa,* a species that may be critical for establishing new fertile islands in the Mojave Desert (cf. McAuliffe 1988). Our manipulations (Fig. 1) compared 5 treatments with various combinations of aboveground shade effects, belowground nutrient effects, and belowground root competition effects of desert shrubs.

METHODS

Study Area

This study was conducted on a bajada (slope) in Lucky Strike Canyon (36°23′N, 115°28′W; 1127 m elevation) on the east side of the Spring Mountain Range, 50 km northwest of Las Vegas, Nevada, in the Mojave Desert of the southwestern United States. The study area includes vegetation typical of regional desert bajadas and is located at the lower elevational boundary of the *Coleogyne ramosissima* Torr. (blackbrush) plant community (found between 1100 and 2000 m elevation in the Mojave Desert) and the upper boundary of a plant community dominated by *Ambrosia dumosa* (Gray) Payne (white bursage; Lei and Walker 1997a, 1997b). *Larrea tridentata* Cov. (creosote bush) is a co-dominant in the *A. dumosa* community. Shrub diversity is higher at this ecotone than at any other elevation on the bajada. Other common species include *Krascheninnikovia lanata, Krameria erecta, Ephedra nevadensis, E. viridis,* and *Acamptopappus shockleyi.* For further descriptions of regional vegetation see Beatley (1975) or Rundel and Gibson (1996). Nomenclature follows Hickman (1993).

Experiments described here are part of a larger study of shrub dynamics on permanent plots distributed along an elevational gradient from 1030 m to 1850 m in Lucky Strike Canyon. The study site is located on a 13-km-long by 2-km-wide bajada with an average vertical slope of <5°. The slope lacks a central drainage channel but has multiple ephemeral channels scattered across the entire bajada that average 1–2 m deep; our study sites were only on the broad, raised benches between washes. Soils of the canyon are limestone-derived with cemented petrocalcic horizons (caliche) beginning at depths of 15–80 cm. Desert pavement and cryptobiotic crusts (cf. Evans and Belnap 1999) are moderately well developed at the site. Lucky Strike Canyon is characterized by hot summers above 35°C and cold winters below –10°C. Summer rainfall usually occurs during thunderstorms in July and August, but most precipitation comes as winter rains that are widespread and may last several days. Snow is occasional and not long lasting, and mean annual precipitation at the site is <200 mm. Precipitation increases with elevation and temperature decreases with elevation (Rowlands et al. 1982). During the study period (March 1995–May 1996) total precipitation and maximum and minimum temperatures were 780 mm, 32°C, and –20°C at Kyle Canyon (2135 m elevation) above Lucky Strike Canyon and 69 mm, 40°C, and –7°C at Corn Creek (880 m elevation) at the base of Lucky Strike Canyon (National Climatic Data Center 1995, 1996). Relative humidity was typically low (<20%) and evaporation high during summer months.

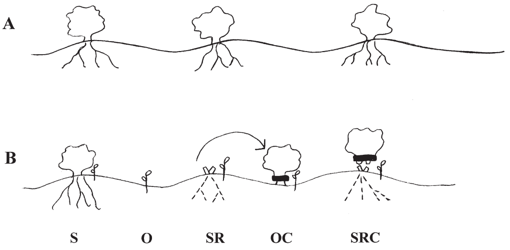

Fig. 1. Diagram of natural pattern of islands of high soil fertility under shrubs and less fertile spaces between shrubs (top) and 5 treatments into which *Ambrosia dumosa* seedlings were transplanted (bottom): S = control shrub, O = control open area, SR = removal of aboveground shrub, OC = addition of cut shrub from SR to an open area, SRC = removal followed by replacement of cut shrub in situ.

Plot Designs, Treatments, and Measurements

We examined responses of soil parameters and of transplanted *A. dumosa* seedlings to experimental removals and additions of *A. dumosa*, *L. tridentata*, and *C. ramosissima* shrub canopies. In March 1995 we randomly selected 24 locations (8 sets of shrubs for each of 3 species) at approximately 15-m intervals along a 360-m transect perpendicular to the slope of the bajada. At each location we selected (within a 10-m radius of the chosen point on the transect) a set of 3 shrubs of the same species and 2 open spaces and initiated the following treatments: unaltered shrub (S); removal of all aboveground portions of a shrub (SR) by clipping stems at ground level; removal as in SR, followed immediately by replacement of the cut shrub in situ with wire tie-downs (shrub removal plus shrub canopy addition; SRC); open surface at least 50 cm from any shrub (O); and addition of SR shrub canopy to an open site with tie-downs (OC; Fig. 1). Stump sprouts from the SR and SRC treatments were removed as needed during the experiment. Less than 15% of cut stumps sprouted.

Immediately preceding the treatments (March 1995) and 7 months following treatment initiation (October 1995), surface soils (0–8 cm deep; A_0 and A_1 horizons) were sampled in each treatment following removal of any loose organic debris (O horizons). Transplanted seedlings were located on the east-northeast side of each shrub to minimize solar radiation; soils were collected first (March) to the south and subsequently (October) to the north of focal shrubs in order not to disrupt transplants. Soils were immediately passed through a 2-mm sieve, then placed in air-tight soil canisters and refrigerated at 5°C prior to analysis within 72 hours of collection.

After removal of 20 g of soil for analysis of nitrogen mineralization, soils were weighed, dried at 105°C to a constant mass, and reweighed to determine soil moisture content and dry mass of sieved fines per volume (an approximation of bulk density). Soil pH was determined with a glass electrode on a 2-g sample of dry soil saturated with 5 mL deionized water (McLean 1982). We used the Bouyoucos hydrometer method (Day 1982) to determine particle size. Organic matter content of soils was determined by mass loss after ignition at 550°C (Black 1965). We took care to avoid higher temperatures that would cause loss of carbonates. After oven-drying, a 0.4-g sample of each soil was digested in sulfuric acid with a mercuric oxide catalyst and then analyzed colorimetrically for total Kjeldahl nitrogen using an automated salicylate procedure (Environmental Protection Agency 1984). We measured dry mass per volume and particle size only in October.

In situ methods for assessing available nitrogen are not suitable for desert soils because water potentials fluctuate greatly between rainstorms and long dry periods (Lajtha and Schlesinger 1986). Laboratory incubations allowed us to compare potential mineralization among treatments, but our values do not represent field conditions. The available nitrogen pool was determined on 10 g of fresh soil after extraction in 100 mL 2M KCl for 4 hours on a shaker. After the soil had settled, we analyzed the supernatant for available N (Keeney and Nelson 1982) using an automated Cd reduction procedure (NO_2 and NO_3) and an automated phenol procedure (NH_4; Alpkem 1991). An additional 10 g of fresh soil was placed in a 40-mL tube that was then filled with distilled water and placed in a 40°C oven for 1 week, after which NH_4 levels were again determined. Water was added as needed to ensure an anaerobic environment. Nitrogen mineralization was then reported as the difference between post-incubation and pre-incubation $NH_4 + NO_2 + NO_3$ concentrations (Keeney 1982, Lober and Reeder 1993).

Ambrosia dumosa seedlings were grown from locally collected seeds in 20-cm-deep cone-shaped containers (77.2 cm^3) in a greenhouse from December 1994 to March 1995. Each potted plant was watered weekly as needed to keep the soil moist until the final month when watering was reduced. Nutrients were applied twice (12 mL Miracle Gro dissolved in 20 L of tap water) during the 4-month period. In March 1995 the largest 252 seedlings (10–18 cm tall) were chosen. Twelve seedlings were removed for initial biomass determination. To ensure survival of at least 1 transplant per replicate, 2 seedlings were planted at each of the 8 replicates of 5 treatments for the 3 species of shrubs (total = 240 seedlings). Where both seedlings per replicate survived transplanting, the smaller one was removed within 6 weeks of planting to ensure survival of 1 seedling per replicate during the 60 weeks of the experiment. Seedlings at each replicate were caged within a cylinder of 0.25-inch (0.63-cm) mesh hardware cloth, 15 cm in diameter and 15 cm (under shrubs) to 30 cm (open sites) tall. Lower edges of the cages were buried and secured with nails to prevent rodent herbivory. Tops of the cages were left open. Only 2 incidents of herbivory were detected. Seedlings were watered (1 L plant^{-1} week^{-1}) for 3 weeks after planting. Seedling heights were measured 12 and 24 weeks after planting. We compared treatment effects on survivorship of seedlings (low survival after 60 weeks precluded destructive harvests).

Statistical Analyses

Soils sampled in March (preceding shrub manipulations) from the shrub and open environments were compared with a MANOVA (SAS 1988), and significant differences between treatments (shrub versus open) or species (*A. dumosa, L. tridentata, C. ramosissima*) were further examined with 2-way ANOVA followed by Student-Newman-Keuls and Tukey tests for multiple comparisons. Soils from October (28 weeks after treatment initiation) were also analyzed with MANOVA followed by 2-way ANOVA to compare treatments (S, SR, SRC, O, and OC) and species. October values for dry mass per volume and particle size were compared with 2-way ANOVA. Transplant heights were analyzed with 2-way ANOVAs. Transplant survivorship was analyzed with a 2-way ANOVA (treatment and species), followed by Kruskall-Wallis 1-way ANOVAs on ranks (treatment, species) using the number of weeks each seedling survived (Sigma Stat 1995). Transplant survivorship was also analyzed by logistic regression of the number of seedlings alive or dead on the last sample date (Sigma Stat 1995). Significance was determined at $P = 0.05$.

RESULTS

Soils

Soils sampled in March (prior to our shrub manipulations) differed by both treatment and species (Table 1). Soil pH, water, organic matter, Kjeldahl nitrogen, and nitrogen mineralization were all higher under shrubs than in adjacent open areas (Tables 1, 2, Fig. 2). Species differences also emerged: soils under *C. ramosissima* had higher pH and lower mineralizable nitrogen than soils under *A. dumosa* shrubs (Table 1, Fig. 2). Soils under *L. tridentata* had pH levels similar to *A. dumosa* and mineralizable nitrogen similar to *C. ramosissima.* There were no species differences in soil water and no significant treatment-by-species interactions in March. Dry mass per volume and particle size (measured only in October) both varied between S and O treatments. Dry mass per volume was higher in open habitats (adjacent to *L. tridentata:* 1.22 ± 0.02 g cm^{-3}; *C. ramosissima*: 1.28 ± 0.03; *A. dumosa*: 1.29 ± 0.03; $P < 0.001$) than in soils under shrubs (*L. tridentata*: 0.98 ± 0.04; *C. ramosissima:* 1.02 ± 0.04; *A. dumosa*: 0.96 ± 0.03). This difference was due to lower sand and silt and higher clay content (less air spaces) in open soils than in soils beneath shrubs (data not shown; $P < 0.01$). Species differences were not found in dry mass per volume, or percent sand or silt, but *C. ramosissima* soils had higher clay content than the other 2 species (data not shown; $P < 0.001$). These soil results not only confirm the presence of islands of fertility under shrubs at the site but suggest that there are species differences in soil characteristics of fertile islands.

In October 1995 both treatment and species effects were again significant in the overall MANOVA (Table 1). Soil organic matter, Kjeldahl nitrogen, and nitrogen mineralization were still higher in shrub-related treatments (S, SR, SRC) than the open (O, OC), but earlier treatment differences in pH and water content were no longer found (Table 1). Species differences were found only in soil water where soils associated with *C. ramosissima* and *L. tridentata* were wetter than *A. dumosa* soils (Tables 1, 2).

Transplants

Mean heights of transplanted *A. dumosa* seedlings did not differ significantly by treatment ($P = 0.37$) or shrub species ($P = 0.86$) 3 or 6 months after planting. Transplant survivorship (Fig. 3) did not differ among species ($P = 0.67$) but did differ among treatments ($P < 0.001$) with the 2-way (parametric) ANOVA. There was no significant interaction between treatment and species ($P = 0.77$). However, assumptions of normality and equality of variances both failed on the 2-way ANOVA.

TABLE 1. Summary table of MANOVA of soil variables for March and October 1995 soil samples. In March, 2 treatments (TRT; open and shrub) were compared. In October, 5 treatments were compared (open, shrub, shrub removal, shrub removal plus shrub canopy addition, and canopy addition). For both dates 3 species (SPP; *Ambrosia dumosa, Larrea tridentata, Coleogyne ramosissima)* were compared. There were no significant treatment-by-species interactions in March ($P = 0.56$; df = 8) or October ($P = 0.15$; df = 8).

			pH		Water		Organic matter		Kjeldahl nitrogen		Mineralizable nitrogen	
Source	MANOVA	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
MARCH												
TRT	0.0001	1	3.05	0.0200	12.2	0.0007	31.75	0.0001	29.62	0.0001	3.55	0.0093
SPP	0.0001	2	6.68	0.0019	1.46	0.2373	1.09	0.3407	0.57	0.5662	17.95	0.0001
OCTOBER												
TRT	0.0001	4	1.19	0.3181	1.07	0.3776	15.39	0.0001	20.87	0.0001	6.35	0.0001
SPP	0.0001	2	1.43	0.2438	20.25	0.0001	2.93	0.0578	2.80	0.0655	1.02	0.3644

TABLE 2. Gravimetric soil water content (percent) for March and October soil samples (mean ± $s_{\bar{x}}$, $N = 8$; treatments are: O = open, S = shrub, SR = shrub removal, SRC = shrub removal and canopy replacement, OC = shrub canopy addition). Statistical comparisons are indicated in Table 1.

Treatment	*Ambrosia dumosa*	*Larrea tridentata*	*Coleogyne ramosissima*
MARCH			
O	13.27 ± 0.25	11.83 ± 0.35	12.88 ± 0.39
S	14.25 ± 0.32	13.36 ± 0.38	13.39 ± 0.32
OCTOBER			
O	0.02 ± 0.01	0.16 ± 0.04	0.17 ± 0.04
S	0.06 ± 0.03	0.19 ± 0.04	0.27 ± 0.08
SR	0.01 ± 0.01	0.16 ± 0.04	0.19 ± 0.05
SRC	0.06 ± 0.03	0.21 ± 0.06	0.21 ± 0.04
OC	0.06 ± 0.04	0.15 ± 0.04	0.27 ± 0.06

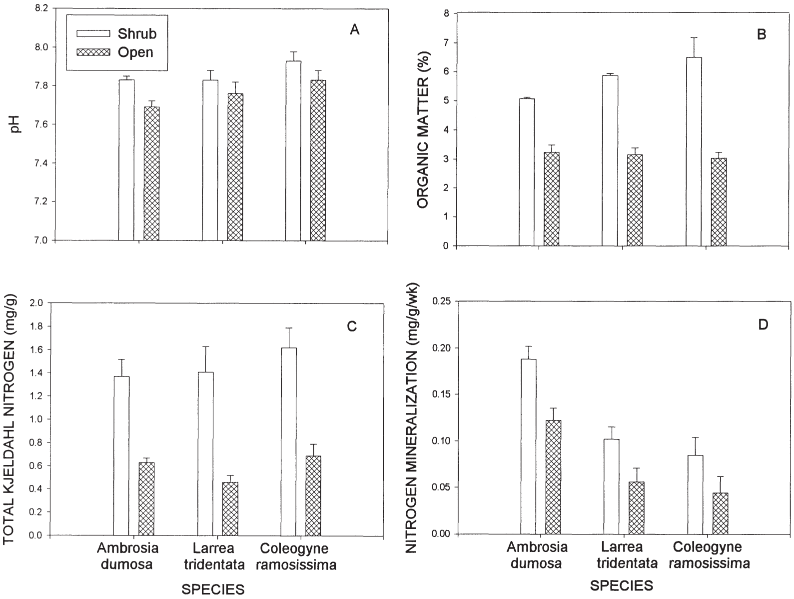

Fig. 2. Values of 4 soil parameters (A: pH; B: organic matter; C: total Kjeldahl nitrogen; D: nitrogen mineralization) for shrub (S) and open (O) treatments associated with 3 shrub species (*Ambrosia dumosa, Larrea tridentata, Coleogyne ramosissima*) from March 1995 samples (prior to treatment initiation; mean ± $s_{\bar{x}}$, $N = 8$). All shrub-versus-open comparisons were significantly different. See text for species differences.

Therefore, we performed subsequent 1-way (nonparametric) ANOVAs on ranks that yielded similar results (species: $P = 0.56$; treatments: $P < 0.001$). Survival was always highest ($P < 0.05$; Tukey and Student-Newman-Keuls multiple comparisons following 2-way ANOVA) in the SR treatment (fertile island but no canopy) followed by the O treatment (neither fertile island nor canopy). Survival was also relatively high in the SRC treatment (fertile island and canopy but no root competition) for *A. dumosa* and *C. ramosissima*. Survival was lowest ($P < 0.05$) in the S treatment for *A. dumosa* and *C. ramosissima* and relatively low for *L. tridentata.* Shrub canopy therefore had the most negative effect (O > OC, SR > SRC), even overriding apparent positive effects of fertile islands (O > SRC). The logistic regression model was rejected, indicating that species and treatment were not good predictors of transplant survivorship.

The influence of soil characteristics on individual seedlings was tested by regressing total weeks of survival against all soil variables and against principal components constructed from combined soil variables. None of these multiple regressions was significant either within or across treatments ($P > 0.20$).

DISCUSSION

The establishment of desert plants is often facilitated by nurse plants that provide shade, fertile soils, and perhaps protection from herbivores for new seedlings (McAuliffe 1984, Franco and Nobel 1989, Callaway and Walker 1997). *Ambrosia dumosa* is able to become established in open desert soils without the aid of a nurse plant canopy (McAuliffe 1988) and may be a critical species for the establishment of other common desert plants such as *L. tridentata*. Understanding what limits establishment and growth of *A. dumosa* seedlings can provide insights into why and how *A. dumosa* can begin a new cycle of fertile island development. Canopy removal experiments in this study not only confirmed the common pattern of fertile islands under desert shrubs, but also detected differences in soil characteristics beneath different species of shrubs. Transplant responses to treatments indicated the positive influence of increased soil nutrients under shrubs but the overall net negative impact of shrubs on *A. dumosa* seedlings through competition (for nutrients, light, and water). These negative impacts may partly

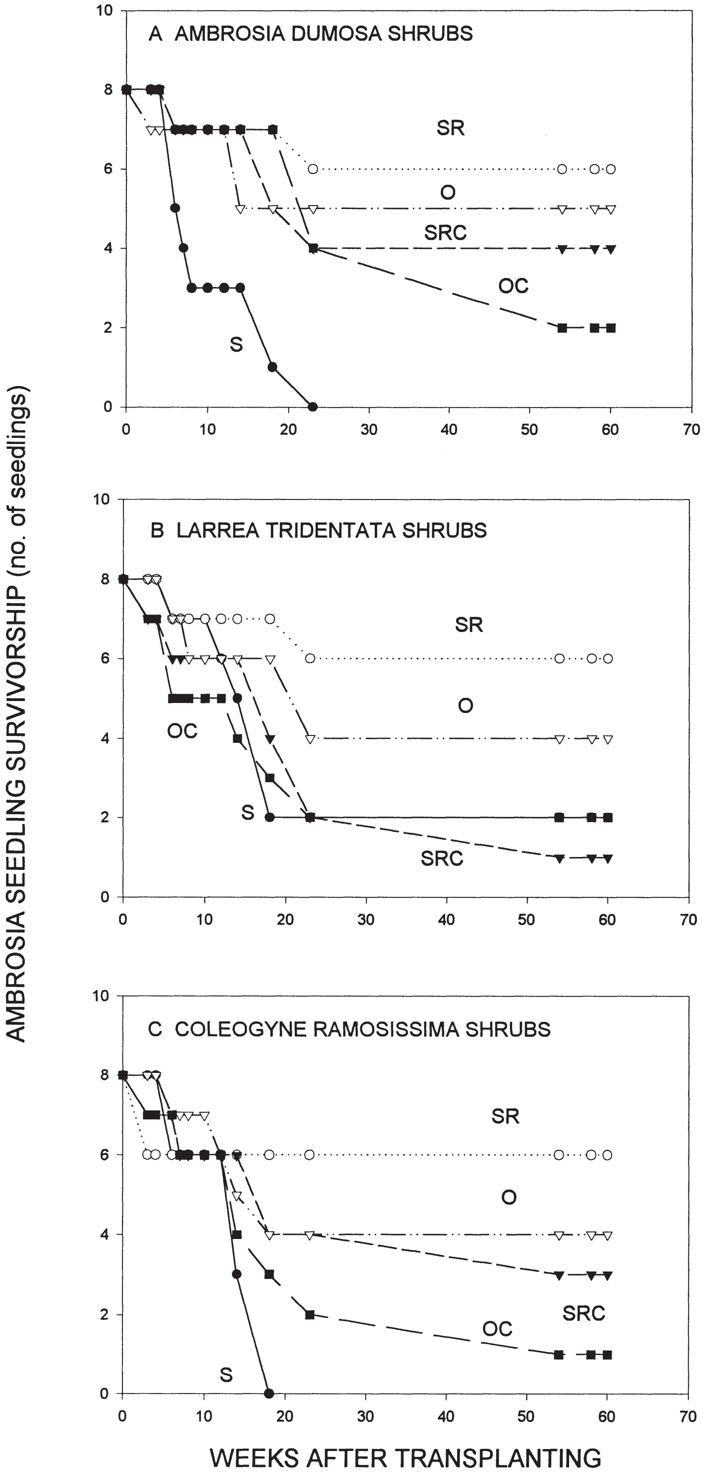

Fig. 3. Survival of transplanted *Ambrosia dumosa* seedlings associated with *Ambrosia dumosa* shrubs (A), *Larrea tridentata* shrubs (B), and *Coleogyne ramosissima* shrubs (C) in the S, O, SR, SRC, and OC treatments described in Figure 1.

explain why *A. dumosa* establishment occurs primarily in open spaces between shrub canopies.

All 7 measured soil variables (pH, water, organic matter, dry mass per volume, particle size, total and mineralizable nitrogen) were more favorable for plant growth under existing shrubs than in adjacent open spaces. These results support conclusions from other studies of fertile islands (e.g., Garcia-Moya and McKell 1970, Charley and West 1975, Klemmedson and Barth 1975, Virginia 1986, Halvorson et al. 1994, Schlesinger et al. 1996) that have found abundant evidence of spatial heterogeneity in soil properties of arid lands. Our values for soil organic matter under shrubs are comparable to another study from Lucky Strike Canyon (2–6%, Lei and Walker 1997b) but higher than other Mojave Desert studies (2–3%, Bolling and Walker 2000; 1.5–4.1%, Rundel and Gibson 1996) where surface organic soils (A_0 horizon) were removed. Our values from the open spaces are also higher than generally reported, perhaps due to the high cover (25%, D. Thompson personal observation) of cryptobiotic crusts in our open sites.

Species differences in soil characteristics were detected among soils collected underneath 3 shrub species. These differences may cause differential survival of *A. dumosa* seedlings, although such differences were not seen in this experiment (see below). In March, soils under *A. dumosa* shrubs had higher rates of nitrogen mineralization than soils under *C. ramosissima* or *L. tridentata.* Considering the additional allelopathic effect that has been demonstrated for *L. tridentata* roots (Mahall and Callaway 1992), *L. tridentata* shrubs may provide the least favorable environment for seedlings. During the drier period in October, soils under *C. ramosissima* were wettest, perhaps reflecting moisture retention of higher clay values under *C. ramosissima.* Organic matter and Kjeldahl nitrogen tended (nonsignificantly) to be different among species in October. Analyses of a larger data set including other elevations (Thompson et al. unpublished data) indicate that soils under *A. dumosa* shrubs have lower organic matter levels than soils beneath *L. tridentata* and *C. ramosissima* shrubs.

Survivorship of *A. dumosa* transplants did not differ among nurse plant species, despite differences in soil characteristics. These results suggest that survival is affected by variables or combinations of variables more important than individual soil variables. Highest survivorship was in the SR treatment for all shrub species, suggesting benefits of the fertile island soil environment (higher nutrients, water, and organic matter) and a high light environment. The fact that *A. dumosa* survivorship was better in SR and SRC than under intact shrubs (S) further suggests a lack of root competition may be important to seedling survivorship (Fig. 4). The next highest survivorship was in the O treatment for all species, suggesting that any of the remaining treatments (S, OC, SRC), each of which includes a shrub canopy, was worse for *A. dumosa* seedlings than the high light but low nutrient environment in the open. The S treatment had lowest *A. dumosa* survivorship, probably due to combined negative effects of shrub canopy and root competition.

Only 39.2% of all transplanted seedlings survived the 60-week period. However, differences in timing of mortality among treatments are likely to have important consequences for seedling establishment. The Mojave Desert is characterized by infrequent and spatially patchy rainfall (Smith et al. 1997). Nearly dry seedlings are able to recover and sprout leaves within days following rainfall (F. Landau personal observation). On average, the longer a seedling can survive through a dry period, the more likely that it will experience rains and survive to become a mature shrub.

Interactions between the effects of light (or presence of shrub canopy) and fertile island soil conditions, and the relative importance of light, nutrients, and root competition, can be inferred from survivorship patterns of the *A. dumosa* transplants. Light appeared to be a limiting factor whether nutrients were low (O > OC) or high (SR > SRC, S). In contrast, nutrients were not limiting at low light (OC > S, no pattern for OC and SRC) but were limiting at high light (SR > O). These patterns suggest the most important factor is the negative effect of shrub canopy presence (Miriti et al. 1998), followed by the positive effect of fertile island nutrients. Root competition (or the presence of live roots) appears to be a 3rd variable that also had a negative effect (SRC > S). Competition for water by nearby adult plants can reduce seedling growth (Fonteyn and Mahall 1981, Fowler, 1986, Nobel and Franco 1986).

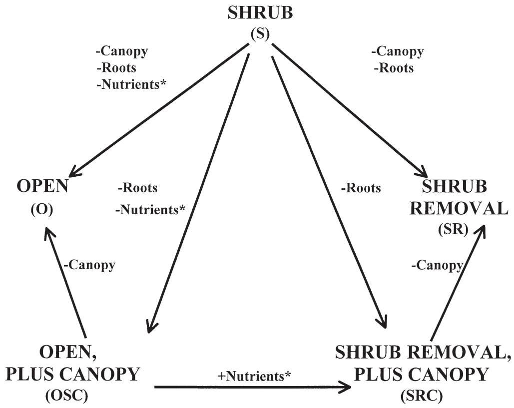

Fig. 4. Summary of how the 5 treatments (S, SR, SRC, OC, O) altered above- (shade and other canopy effects) and belowground (nutrients, roots) environments for transplanted *Ambrosia dumosa* seedlings. Asterisk implies addition or subtraction of not only nutrients but other soil properties of fertile islands.

Shade is normally considered advantageous to seedling establishment in deserts because it reduces temperature extremes and water loss.

Although we took no light measurements in this study, we did measure photosynthetic photon flux density (using a Licor 1000) 5 months after initiation of identical treatments with *A. dumosa* in a later experiment at the same site (May 1998). Despite leaf loss, the SRC (mean ± $s_{\bar{x}}$: 398 ± 43 micromoles m^{-2} sec^{-1}; $N = 30$) and OC (414 ± 42) treatments remained as shaded as the intact shrubs (S treatment: 492 ± 42) and all 3 "shrub" treatments were significantly more shaded than open treatments (O: 1009 ± 42; SR: 1004 ± 42). Branches of *A. dumosa* (and equally dense branches of *C. ramosissima*) apparently provided nearly as much shade as leaves and branches combined. In contrast, *L. tridentata* has a very low leaf area index (Chew and Chew 1965, Smith et al. 1997), so leaf loss presumably does not markedly increase light transmission to the ground.

Soil moisture is considered to be a critical environmental variable affecting establishment and growth of desert plants and may affect nutrient availability (e.g., nitrogen is limiting only when water is plentiful; Fisher et al. 1988, Sharifi et al. 1988, Lajtha and Whitford 1989). This experiment was initiated during a wet spring, and the March soil samples were collected 2 days after a rainstorm. Following rains in late May (10 weeks after transplanting), there was a 28-week drought. During this drought most *A. dumosa* transplant mortality occurred. There was no significant correlation between October gravimetric soil moisture at each transplant and individual transplant survivorship (P-values ranged between 0.30 and 0.70). More detailed measurements might have helped explain survivorship in terms of soil moisture because gravimetric soil content may not closely reflect water available for plant growth. Nevertheless, driest habitats (SR, O) had highest survivorship and the wettest habitat (S) had lowest survivorship, suggesting that in a drought water is not as limiting as light (or absence of shade). Therefore, our results during a drought may be typical of the dynamics of seedling establishment in more mesic periods as well. Alternatively, shrub roots may have been so efficient at removing available water (Fonteyn and Mahall 1981, Hunter 1989) that the below-shrub environment was actually too dry for seedlings during our study. In wetter years root competition from the shrub may be less detrimental to seedling establishment.

Species differences in soil water were present only in the dry (October) sampling period (*C. ramosissima* = *L. tridentata* > *A. dumosa*). Canopy architecture might help explain why *L. tridentata* soils were wetter than *A. dumosa* soils in the dry season. The canopy of *L. tridentata* is shaped like an inverted cone (Ludwig et al. 1975), and this shape may maximize condensation of water vapor and stem flow from its relatively tall, spreading branches. However, this shape also allows soil surface evaporation because of the openness of the surface beneath it; *A. dumosa* and *C. ramosissima* are hemispherical in shape with foliage almost to the ground, reducing loss from surface evaporation. Therefore, other explanations such as more efficient water extraction by *A. dumosa* roots (D. Neuman personal communication) must also be considered.

Ambrosia dumosa seedlings survived better in the open (O) than under shrubs (S), supporting McAuliffe's (1988) assertion that *Ambrosia* is a colonizer of open habitats. When it does colonize under shrubs (or in exposed fertile islands caused by shrub mortality), it has a different set of environmental characteristics to cope with under each shrub species. For example, Smith et al. (1987) found that artificial shade in the Sonoran Desert increased soil nutrients in both shrub canopies and open desert, but patterns of increase differed between *A. deltoidea* and *L. tridentata* shrubs. Differential responses to these variations in microsite ultimately impact distribution and zonation of desert shrub species. Our study site, at the ecotone between *A. dumosa*– and *C. ramosissima*–dominated communities, is the type of environment where shrub species replacements are most likely to lead to shifts in community composition along the elevational gradient. For example, the lower boundary of *C. ramosissima* in the Mojave Desert has shifted at least 100 m several times in the last 1000 years (Cole and Webb 1985, Hunter and McAuliffe 1994). Current studies are addressing how responses to shrub removals vary at different elevations in Lucky Strike Canyon and how episodic recruitment of *L. tridentata* and *C. ramossisima* seedlings is affected by shrub species and shrub-induced microsites.

McAuliffe (1988) proposed that the establishment of seedlings of *A. dumosa* in open areas may initiate fertile island development where this species occurs in arid regions of southwestern United States. We have demonstrated that 3 interacting variables (shade, nutrients, roots; Fig. 4) affect the initial survival of *A. dumosa* seedlings. However, shrubs differ in their soil chemistry and may provide unique habitats for seedling establishment. Removal of a shrub with retention of the fertile island beneath it provided the best environment for *A. dumosa* seedling establishment (light and nutrient addition), followed by open habitats (light addition). Shaded habitats with or without nutrients were poorer habitats for establishment, and the intact shrub environment (minus light, nutrient addition, root competition) was the worst environment. These results provide a mechanistic explanation for McAuliffe's hypothesis and suggest *A. dumosa* establishment will be most likely to occur in open habitats that have some nutrient enrichment.

ACKNOWLEDGMENTS

We thank our numerous field assistants, including J. Alexander, C. Brundy, J. Cleverly, C. Heyne, T. Keller, S. Lei, F. Martin, J. Piorkowski, L. Stark, and M. Turner. J. Bolling, D. Dean, T. Keller, and S. Vrooman helped with lab analyses. Further welcome advice was provided by J. Brown, J. Cole, P. Medica, J. McAuliffe, M. McGill, and W. Whitford. Partial funding was provided by NSF grant EPS-93-53227 and a grant from the University of Nevada, Las Vegas Grants and Fellowship Committee. The manuscript was improved by comments from K. Lajtha, K. Owens, S. Smith, J. Titus, and an anonymous reviewer.

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Received 20 September 1999
Accepted 7 January 2000

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Author(s): David E. Brown and Richard A. Minnich
Source: *American Midland Naturalist*, Vol. 116, No. 2 (Oct., 1986), pp. 411-422
Published by: The University of Notre Dame
Stable URL: http://www.jstor.org/stable/2425750

Fire and Changes in Creosote Bush Scrub of the Western Sonoran Desert, California

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ABSTRACT: Seven years of above normal precipitation between 1976 and 1983 encouraged heavy growth of native annuals and exotic grasses in the western Sonoran Desert. Unprecedented fires in creosote bush scrub started mostly after 1978. Analysis of several burns near Palm Springs revealed that most shrubs, including *Larrrea tridentata, Ambrosia dumosa* and *Opuntia* spp., are poorly adapted to relatively low intensity fires as evidenced by limited sprouting and reproduction. These shrubs were replaced by open stands of *Encelia farinosa*, native ephemerals, and European exotics, mostly *Bromus rubens* and *Schismus barbatus*. The rapid selective thinning of creosote bush scrub species suggests that the modern biogeography of this ecosystem may be controlled, in part, by recurrent burning.

INTRODUCTION

Fires are infrequent in the Sonoran Desert owing to limited biomass, wide spacing between shrubs and sparse ground cover (Humphrey, 1949, 1962). Recent studies in Arizona (Rogers and Steele, 1980) and California (Tratz and Vogl, 1977: Tratz, 1978; O'Leary and Minnich, 1981) indicate that many desert perennials are poorly adapted to burning. Successional studies in creosote bush scrub reveal postdisturbance recolonization by long-lived species is very slow initially and may require hundreds of years (Vasek, 1980, 1983). Thus rare fires may have long-term impact on the structure and composition of this community.

Heavy growth of native and exotic annual vegetation promoted by extraordinarily heavy precipitation between 1976 and 1983 resulted in unprecedented fires in creosote bush scrub vegetation along the western margins of the Mojave and Sonoran deserts of southern California. This study documents fire and early postfire succession in creosote bush scrub in several burns near Palm Springs, and it evaluates the stability and biogeography of this ecosystem in relation to recurrent fire.

STUDY AREA

Four sites on Quaternary alluvial fans descending from the E scarp of the San Jacinto Mountains at the end of the Coachella Valley near Palm Springs, California, were chosen for study (Fig. 1). Coarse-textured soils are well-drained, moderately alkaline with a minimum of organic matter (Fraser, 1931; Proctor, 1968; Knecht, 1980).

The climate of the Coachella Valley is extremely arid owing to its subtropical latitude and to rain shadows of the San Jacinto Mountains (Bailey, 1966). Average annual rainfall at Palm Springs, mostly from winter cyclonic storms, is 138 mm (Table 1). Summers are hot and dry, although tropical moisture from the equatorial Pacific produce occasional thunderstorms, mostly over the nearby mountains.

VEGETATION

Most of the Sonoran Desert is covered with creosote bush scrub consisting of scattered low shrubs less than 2 m. Representative growth forms include evergreen

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sclerophyllous and deciduous shrubs, subligneous subshrubs, leaf and stem succulents, and annual herbs (Johnson, 1974; Burk, 1977). Bajadas and adjacent mountainsides in the Coachella Valley are covered by *Larrea tridentata*, *Encelia farinosa*, *Hilaria rigida*, *Enchinocereus engelmannii*, and *Krameria grayi*. Vegetation on the plains and lower bajadas, including the study sites, is dominated by *L. tridentata*, *Ambrosia dumosa* and *E. farinosa*, which may form 60-100% of total vegetation cover (McHargue, 1973; Shreve and Wiggins, 1964). *Cercidium floridum*, *Olynea tesota*, *Dalea spinosa*, *Beloperone californica* and *Hyptis emoryi* are common along washes. Succulents such as *Ferocactus acanthodes*, *Echinocereus engelmannii*, *Opuntia basilaris*, *O. bigelovii* and *O. echinocarpa* reach maximum densities on sandy hillsides and bajadas with rocky, gravelly, or sandy substrates (McHargue, 1973).

FIRE HISTORY

Until the last decade, burning was almost unknown in the area (Fig. 1). Two large fires in 1911 and 1945 burned chaparral and mixed evergreen forests above 1200 m. A 3600-ha fire on the N slope of Mt. San Jacinto in 1973 spread into a small area of creosote bush scrub (O'Leary and Minnich, 1981). Two rare Mexican west coast tropical storms (September 1976, August 1977), followed by abnormally stormy winters from 1977-1978 to 1979-1980 and 1982-1983, caused sustained above-normal precipitation

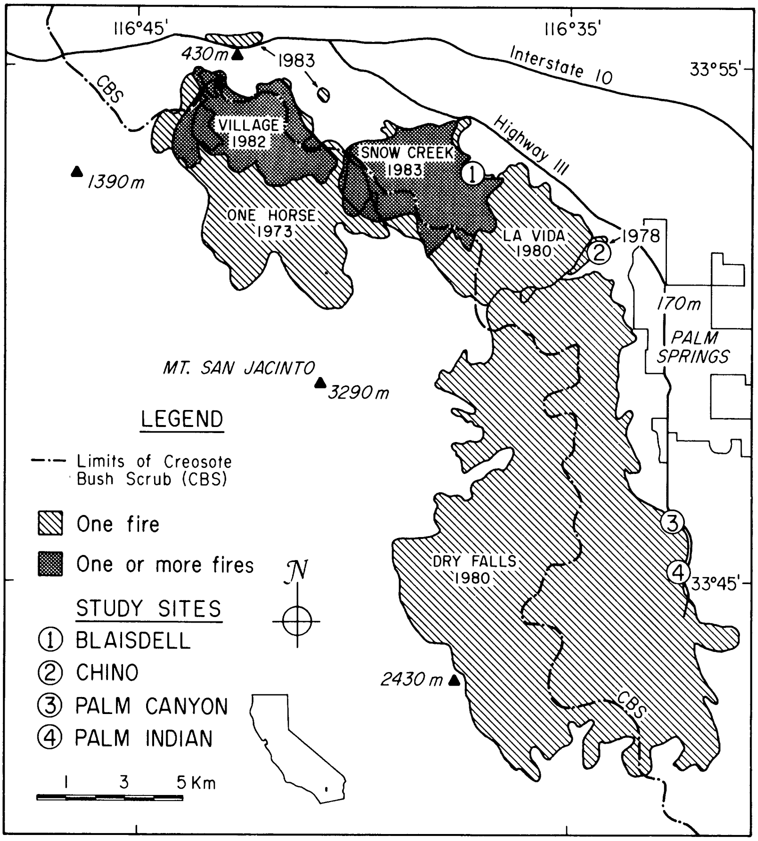

Fig. 1.—The study sites and fire perimeters. Limits of cresote bush scrub are interpreted from 1:30,000 scale aerial photography (1971) on file at the Department of Earth Sciences, University of California, Riverside

(Table 1) which encouraged heavy growth of shrubs and herbaceous understory. Beginning in 1978, a series of fires spread through dried herbaceous fuels into extensive areas of creosote bush scrub, including the Chino Canyon fan (500 ha, 1978), Blaisdell and Chino canyons (2800 ha, 1980), and the E scarp and alluvial fans below 1300 m from Chino Canyon S to Palm Canyon (6000 ha, 1980). A 1200-ha burn in 1982 overlapped large areas burned in 1973 near Snow Creek. In 1983, the first of three fires reburned portions of Snow Creek and Blaisdell Canyon. Two smaller fires also occurred along Snow Creek road and Interstate 10.

The fires in creosote bush scrub characteristically spread during periods when ambient temperatures averaged 35-40 C and relative humidity ranged from 10-25%. High winds (10-20 ms^{-1}) were caused by the typical spring and early summer gravity acceleration of descending coastal marine air spilling through San Gorgonio Pass. Upcanyon winds and nocturnal air drainage promoted fire spread on the eastern face of Mt. San Jacinto. The flames reduced the herb layer to a low stubble, indicative of fast-moving, low-intensity fires.

SITE SELECTION AND METHODS

Four sites were located on relatively homogeneous terrain (*i.e.*, avoiding large washes or rock outcrops) at the fire boundaries on the Chino, Blaisdell and Palm Canyon alluvial fans in order to compare burned vegetation with adjacent unburned stands (Fig. 1). The areas were surveyed between 25 April and 27 May 1983, when desert annuals were declining and perennials were in full growth or flower.

Perennial and annual plants were analyzed separately, with major emphasis placed on perennial cover and density. In unburned transects, the vegetation sampled is assumed to represent the prefire state of burned areas. In each site, two 100-m parallel transects were employed in burned and unburned areas (200 m for each). Both belt and line methods of sampling were used along each 100-m transect (Mueller-Dombois, 1974). The line intercept method was used to obtain percent cover (intercept distance) and density of perennial species (*cf.* Canfield, 1942). Each plant along the intercept was measured, identified and counted. Seedlings on each intercept were counted as part of total perennial cover, and were also noted separately. Belt transects (100 m x 1 m) were used to determine seedling density. Seedlings were counted and time of establishment was assigned as first postfire growing season (older plants > 5 cm height) or later growing season (< 5 cm). A 1-m-sq area was located at the end point of each transect to estimate herbaceous cover and floristic composition.

In transects within the burns, surviving plants, sprouting behavior and mortality (fire-killed snags) were recorded. Fire damage was estimated by qualitatively ranking plants as burned, scorched or green. Burned plants showed pyrolysis of foliage and fine

TABLE 1.—Annual precipitation at Palm Springs (source: California 1984)

Season	Total (mm)	Percent of normal
1889-1983 Mean	138	
1976-1977	174	126
1977-1978	289	209
1978-1979	188	136
1979-1980	412	299
1980-1981	64	46
1981-1982	98	71
1982-1983	222	161

stems, leaving a stump or main stems. Scorched plants retained all or most branches and dried foliage. Green plants retained living foliage or escaped fire entirely. In belt transects, plant snags were counted and ranked for fire damage and recovery. Seedlings were counted in each meter and assigned establishment dates as in unburned areas.

RESULTS

The vegetation was sampled 3 growing seasons after burns at Blaisdell, Palm Canyon and Palm Indian sites and after 5-growing seasons at the Chino site. However, data for Chino were merged with other data because there was insufficient data from the single 1978 site to extrapolate small differences in succession from species composition which may be more related to site than temporal changes associated with age class. Nineteen perennial and 10 herb species were recorded.

UNBURNED VEGETATION

Unburned perennial cover averaged 21% and was dominated by *Larrea tridentata*, *Ambrosia dumosa*, and *Encelia farinosa* (Table 2). Wash species (*Acacia greggii*, *Beloperone californica*, *Hyptis emoryi*) and cacti (*Opuntia acanthocarpa*, *O. bigelovii*) were occasional in all sites. Native herb cover (*Aristida adscensionis*, *Chaenactis fremontii* and *Chorizanthe brevicornu*) varied greatly while the European exotics, *Bromus rubens* and *Schismus barbatus*, were nearly everywhere (Fig. 2).

BURNED VEGETATION

Fire damage to perennials.—Most perennials were scorched, although the majority of shrubs were locally burned in several sites, particularly the Blaisdell fan. The pattern of shrub damage was species-specific, suggesting that the combustion of shrubs was more influenced by individual species morphology and fuel properties than spatial variations in fire behavior (Table 3). *Larrea tridentata* was typically only scorched despite its resinous foliage and the dense herbaceous cover growing in organically rich eolian sedimentary mounds beneath. Most main stems were unburned and often contained green foliage. Flame heights from herbaceous fuels were apparently insufficient to burn *L. tridentata* canopies owing to limited herbaceous fuels, limited foliar dead fuel content, and spreading branch habit (low fuel continuity). *Encelia farinosa* was mostly scorched due to the morphology of pencil-thick branches which support an umbrella of leaves with few stems beneath. Only leaves and branches near the ground burned, leaving foliage on ultimate stems. *Ambrosia dumosa* regularly burned because the canopy comprises numerous small branches with a finely divided branching pattern close to herbaceous fuels which maximizes fuel continuity, surface to volume ratio and rapid pyrolysis.

The cacti, including *Opuntia acanthocarpa*, *O. bigelovii*, and *Ferocactus acanthodes*, were normally scorched. The dense spines of *O. bigelovii* tended to carry flames up the crown. *Beloperone californica* and *Hyptis emoryi* were usually less damaged than other shrubs, perhaps owing to higher fuel moisture content in wash habitats. *Hyptis emoryi* is characterized by an upward branching habit, and its upper stems extended above flames. Among infrequent shrubs (data not shown), *Acacia greggii* and *Dalea californica* rarely burned because of their arboreal and semideciduous growth habits. *Bebbia juncea*, *Ephedra californica* and *Krameria grayi* normally burned due to their low growth habits and compact crowns.

Sprouting and mortality. Sprouting of most perennials was limited and depended upon local fire intensity. At the heavily burned Blaisdell site, for example, most plants were reduced to ash and mortality was nearly universal; sprouting was intermittent among scorched shrubs at the other sites (Table 3).

Burned shrubs of most species sprouted less than scorched ones. *Larrea tridentata*, *Ambrosia dumosa* and *Encelia farinosa* rarely sprouted even among scorched individuals that retained full canopy foliage. Many *L. tridentata* shrubs with living foliage after burning died later, presumably as a result of basal cambium damage. Scattered resprouts of *Opuntia acanthocarpa*, *O. bigelovii*, *Echinocereus engelmannii* and *Ferocactus acanthodes*

TABLE 2.—Density (D) and cover (C) of established (unburned) and resprouting (burned) shrubs. Density is expressed in number of plants per 100 m², cover in percent ground covered

	Blaisdell				Chino				Palm Canyon				Palm Indian			
	Unburned		Burned		Unburned		Burned		Unburned		Burned		Unburned		Burned	
Species	D	C	D	C	D	C	D	C	D	C	D	C		C	D	C
Larrea tridentata	2.5	3.1	0	0	3.5	3.4	0	0	3.0	4.2	0	0	8.0	13.4	0	0
Ambrosia dumosa	20.0	13.0	0	0	8.0	4.1	0	0	6.0	4.1	1.5	3.3	5.5	1.7	.5	.2
Encelia farinosa	1.0	.9	0	0	11.5	9.2	1.5	2.0	13.0	10.6	2.0	2.6	3.0	1.4	2.5	3.5
Opuntia acanthocarpa	3.0	1.2	0	0					3.0	1.7	1.0	.3	1.0	.2	0	0
O. bigelovii													7.5	1.2	2.0	.5
Hyptis emoryi					0	0	1.0	.8	2.5	3.0	1.0	.7	1.5	1.6	1.0	.6
Krameria grayi	2.5	1.5	0	0	.5	.3	0	0								
Dalea californica	1.0	.4	0	0												
Mirabilis bigelovii	.5	.3	0	0												
Beloperone californica					3.5	2.0	7.0	3.7								
Hilaria rigida					1.0	.5	0	0								
Ferocactus acanthodes					.5	.1	0	0								
Acacia greggii									0	0	.5	1.4				
Bebbia juncea													.5	.9	.5	.6
Echinocereus engelmannii													.5	.1	0	0
Total	30.5	20.4	0	0	28.5	19.6	9.5	6.5	27.5	23.6	6.0	8.3	27.5	20.5	6.5	5.4

were surrounded by numerous skeletons of dead individuals. The wash species *Beloperone californica* and *Hyptis emoryi* exhibited well-developed stump and crown sprouting. *Acacia greggii* resprouted to former canopy cover within 3 years.

SEEDLING ESTABLISHMENT

More shrub seedlings established on burned than on unburned sites, although the pattern of regeneration varied with species and annual precipitation (Table 4). *Encelia farinosa* accounted for most of the seedlings observed during the first growing season, especially in burns. Most reproduction during the first growing season was composed of *Encelia farinosa*, primarily in burns. *Hilaria rigida*, *Opuntia acanthocarpa* and *Trixis californica* seedlings were observed in burns only after the first growing season (1980-1981). *Mirabilis bigelovii*, *Sphaeralcea emoryi* and *Bebbia juncea* also reproduced in burns mostly during the first growing season, but establishment persisted into later growing seasons. *Ambrosia dumosa* and *Ditaxis lanceolata* establishment increased in later growing seasons. Most

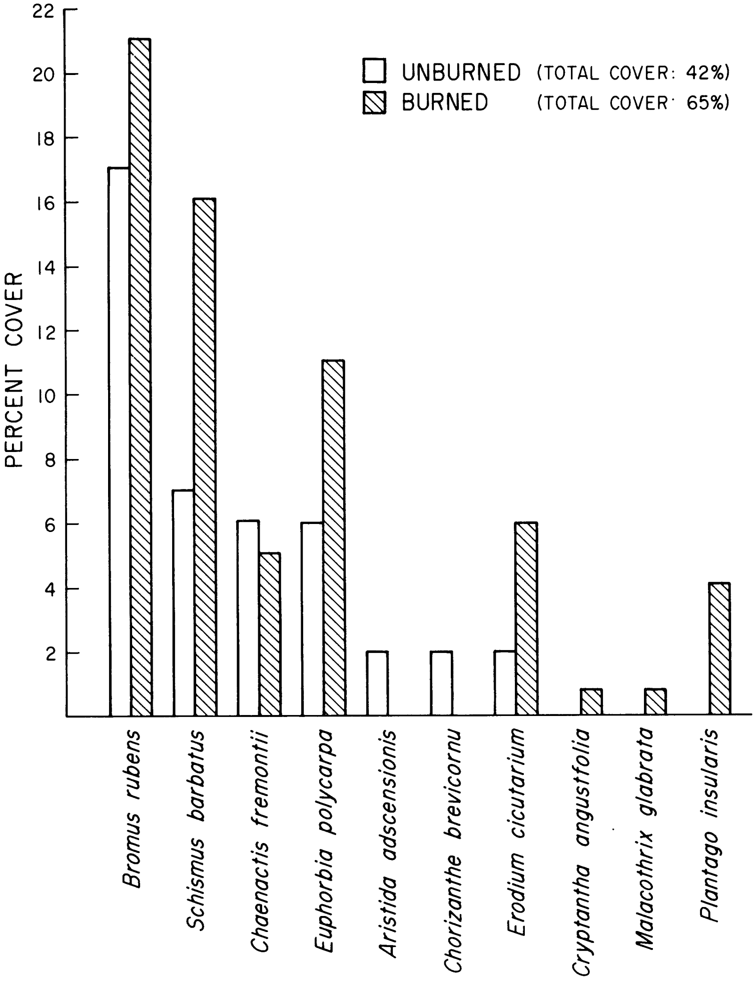

Fig. 2.—Herbaceous cover in burned and unburned sites

seedling reproduction in unburned sites was *E. farinosa* and *A. dumosa*. There was sporadic establishment of *Larrea tridentata* and *Hyptis emoryi*, mostly in unburned sites. The wet 1982-1983 season was followed by abundant reproduction of *E. farinosa* and lesser amounts of *A. dumosa* in both burned and unburned sites.

With the exception of *Encelia farinosa*, seedling densities were less than the density of established shrubs in unburned areas. Severely burned areas with few surviving perennials, such as the Blaisdell fan, had fewest seedlings (Table 2). Several infrequent perennials established no seedlings in the area, including *Acacia greggii*, *Dalea californica*, *Echinocereus engelmannii*, *Ephedra californica*, *Ferocactus acanthodes*, *Frameria grayi* and *Opuntia bigelovii* (removal of adults limited vegetative reproduction in the latter).

CHANGES IN STAND COMPOSITION

The primary effect of recent burns was the reduction of perennial cover, owing to limited sprouting combined with scarce seedling establishment of most shrubs (Fig. 3). After 3-5 growing seasons, the total cover in burned sites was about half that of unburned sites and was composed mostly of *Encelia farinosa*. The largest change was the reduction of *Larrea tridentata* because it experienced almost no sexual or asexual reproduction or resprouting.

Table 3.—Shrub damage, sprouting and mortality (percent)

Species	N	Burned	Resprouts	Scorched	Resprouts	Green	Resprouts	Mortality
Encelia farinosa	122	20	0	78	5	2	2	93
Ambrosia dumosa	84	81	2	16	6	3	3	89
Opuntia bigelovii	49	4	0	94	6	2	2	92
O. acanthocarpa	36	11	0	89	8	0	0	92
Larrea tridentata	35	0	0	100	3	0	0	97
Hyptis emoryi	10	0	0	100	40	0	0	60
Beloperone californica	7	0	0	100	57	0	0	43

Table 4.—Seedling density in initial and subsequent growing seasons

Species	Burned Area 1980-1981* growing season (number/ha)	Burned Area 1981-1983* growing seasons (number/ha)	Unburned Area 1980-1981* growing season (number/ha)	Unburned Area 1981-1983* growing seasons (number/ha)
Encelia farinosa	1460	7010	90	5650
Hyptis Emoryi	90	50	10	30
Mirabilis bigelovii	90	40	0	0
Hilaria rigida	80	0	0	0
Ambrosia dumosa	*60*	*160*	*30*	*200*
Sphaeralcea emoryi	50	10	0	0
Bebbia juncea	50	30	0	0
Beloperone californica	40	40	0	0
Opuntia acanthocarpa	30	0	0	0
Ditaxis lanceolata	10	60	0	0
Trixis californica	10	0	0	0
Larrea tridentata	0	10	0	40

*At the Chino site, the first growing season was 1978-1979. Later growing seasons are 1979-1983

Postfire herb cover averaged 23% greater in burned than unburned stands. *Malacothrix glabrata*, *Cryptantha angustifolia* and *Plantago insularis* were found only in burned areas. Most cover was of exotic European annuals *Bromus rubens* and *Schismus barbatus* (Fig. 2).

DISCUSSION

Fire mortality and postfire succession in creosote bush scrub at Palm Springs are similar to other studies in the Sonoran Desert (Rogers and Steele, 1980; O'Leary and Minnich, 1981). Sprouting behavior of *Larrea tridentata* in the Sonoran Desert was varia-

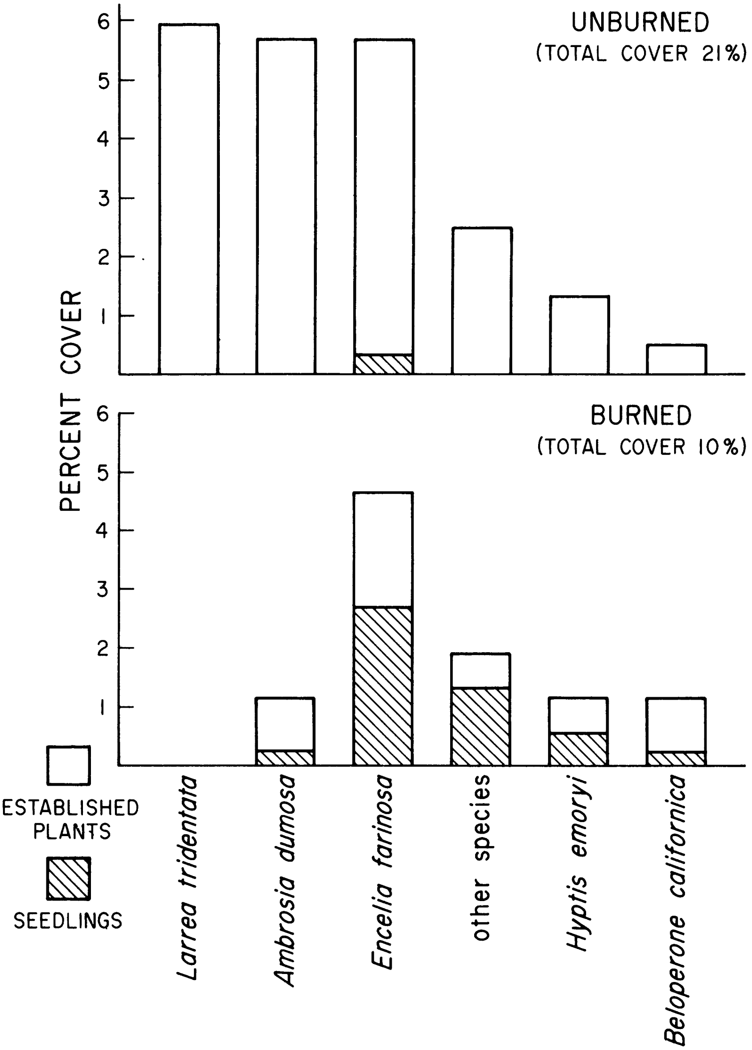

Fig. 3.—Perennial cover in burned and unburned sites (cover expressed in absolute percentages). "Other species" include *Acacia greggii*, *Bebbia juncea*, *Dalea californica*, *Echinocereous engelmannii*, *Ephedra californica*, *Ferocactus acanthodes*, *Hilaria rigida*, *Krameria grayi*, *Opuntia acanthocarpa* and *O. bigelovii*, *Ditaxis lanceolata*, *Mirabilis bigelovii*, *Spheralcea emoryi* and *trixis californica*

ble, depending primarily on fire intensity and season. Dalton (1962) found that slightly to moderately burned *L. tridentata* near Tucson, Arizona, experienced 60-70% mortality. Rogers and Steele (1980) observed minimal resprouting of *L. tridentata*. However, fire intensity and season were not reported. White (1968) found that *L. tridentata* mortality was related to season of burning, with highest mortality prior to the onset of the summer precipitation season. Increased fire intensity and duration also resulted in decreased sprout production.

At Palm Springs, sprouting of *Larrea tridentata* was highly variable in burns which occurred from June through September. O'Leary and Minnich (1981) found moderate sprouting following the July 1973 burn. We observed nearly 100% sprouting following a small burn near Snow Creek in June 1983, but heavy mortality in another burn 2 weeks later 10 km NW. The 1980 burns (July, August-September) caused heavy mortality. These trends indicate that sprouting rates are more related to fire intensity than season of burning.

Heavy *Encelia farinosa* and *Ambrosia dumosa* mortality at Palm Springs parallels findings in Arizona (*A. deltoides*: Rogers and Steele, 1980) and California coastal sage scrub (Malanson and O'Leary, 1982). The reduction of *Opuntia acanthocarpa*, and *O. bigelovii* is comparable to that in burns at Snow Creek (O'Leary and Minnich, 1981), the Borrego Desert (Tratz and Vogl, 1977), and Arizona (Rogers and Steele, 1980). The vigorous sprouting of wash species (*Hyptis emoryi*, *Beloperone californica*, and *Acacia greggii*) at Palm Springs was also observed in similar habitats in the Borrego Desert (*Chilopsis linearis*, *A. greggii*, Tratz and Vogl, 1977). Such sprouting behavior may be a generalized adaptation to flash flood disturbances (Tratz, 1978; Zedler, 1981).

Poor seedling establishment at Palm Springs is probably unrelated to seed availability since all species occur in adjacent unburned areas. Most are capable of long-range seed dispersal by wind (*Larrea tridentata*, *Ambrosia dumosa* and *Encelia farinosa*) or fauna (*Opuntia bigelovii* [vegetative reproduction], *O. acanthocarpa*, *Hyptis emoryi* and *Beloperone californica*) (Ridley, 1930). Scattered resprouts and unburned individuals throughout the burns provide local seed sources. Thus, postfire habitats were apparently unfavorable for establishment.

Reproduction may be encouraged by disturbance. In powerline and road construction disturbances in the Mojave Desert, seedling establishment was most prolific among short-lived species, primarily *Encelia frutescens*, while germination of most long-lived species, including *Larrea tridentata* was limited (Vasek, 1980). We found no evidence of abundant *L. tridentata* reproduction, as reported in Arizona burn sites (Dalton, 1962). In an investigation following severe flooding near Ocotillo, Calif., Zedler (1981) recorded abundant reproduction of *Ambrosia dumosa*, *E. farinosa*, *Larrea tridentata*, *Opuntia echinocarpa*, *Acacia greggii*, *Hyptis emoryi* and *Beloperone californica*. Since postfire establishment was limited in the Palm Springs sites, prolonged surface moisture from abundant rainfall or floodwaters may be required for comparable germination and establishment.

Season of rainfall may have inhibited establishment of several shrubs. In Joshua Tree National Monument (50 km NE), Went (1948) found that *Acacia greggii*, *Dalea* spp., *Hymenoclea salsola*, *Hyptis emoryi* and *Larrea tridentata* germinated only in summer. Beatley (1974) suggested that summer rainfall is a requirement for successful germination of *L. tridentata*. However, unusually heavy summer rains at Palm Springs in August 1979 (44 mm), and the two wettest summers of the century (1983, 1984) resulted in only sporadic establishment of these shrubs. Similarly, Vasek (1980) found only limited germination of long-lived shrubs and succulents, including *L. tridentata*, *Opuntia acanthocarpa*, *Krameria grayi*, *Hilaria rigida*, in the Mojave Desert, despite favorable climatic conditions. *Encelia farinosa* responded prolifically to heavy winter rains of 1982-1983, a trend consistent with its distribution in coastal sage scrub of coastal southern California where summer rain is nearly absent. Zedler (1981) also observed heavy summer germination of this scrub.

Vasek (1980) suggested that soil condition, primarily the accumulation of organic matter, is important for germination. Many perennials at Palm Springs established seedlings only in burns. *Encelia farinosa* and *Ambrosia dumosa* establishment was also initially stimulated in burns. However, both shrubs colonized both burned and unburned sites after the wet 1982-1983 winter.

Desert succession studies elsewhere in California (Vasek *et al.*, 1975a, b; Vasek, 1980, 1983) indicate that most long-lived shrubs (*Larrea tridentata*, *Ambrosia dumosa*, *Opuntia bigelovii*, *Echinocereus engelmannii*, *Acacia greggii* and *Krameria parvifolia*) are characterized by limited but continuous establishment and thus respond negatively to disturbance. The chronic disturbance of desert habitats by wind and water erosion permits suitable sites for both short- and long-lived perennials. Creosote bush scrub stands are reported to occur in various successional states indicating continuous establishment. Postdisturbance regeneration may take hundreds of years to complete, being very slow at first (Vasek, 1980). The scale of such disturbances, however, is much smaller than wildland fires which can remove plant cover over extensive areas and exacerbate reestablishment by long-range seed dispersal.

The limited period of succession considered here permits only speculation on the future postfire succession at Palm Springs. Long-lived species were nearly eliminated and replaced by short-lived shrubs, mostly *Encelia farinosa*, with wash species persisting locally through sprouting. To date, there is little evidence of continuous long-lived perennial replacement as reported by Vasek *et al.* (1975b), in spite of favorable conditions provided by abnormally heavy precipitation. Indeed, 1984 aerial photographs (1:24,000; Riverside County Flood Control) indicate that *Larrea tridentata* has been removed from extensive areas of the San Jacinto Mountains. An open *Encelia farinosa* community now covering the slopes may persist for decades.

FIRE, CREOSOTE BUSH SCRUB STABILITY AND BIOGEOGRAPHY

In contrast with fire-prone chaparral and forest ecosystems covering the mountains of coastal California, many desert perennials appear unable to persist after burns by surviving fires, sprouting, fruit serotiny, long-term seed viability and immediate germination by scarification of soil seed (*see* reviews by Hanes, 1977; Wright, 1982; Reid and Oechel, 1984). Indeed, the rapid transformation of perennial cover and floristic composition of stands in the Palm Springs burns suggests that many creosote bush scrub taxa are poorly adapted to recurrent burning. Recurrent fire appears to select for short-lived desert shrubs, notably *Encelia farinosa* and *Ambrosia dumosa*, at the expense of long-lived species. At the Blaisdell site, the 1983 burn was carried entirely by herbs and eliminated the few shrubs which survived the 1980 burn. Field observations indicate that *Larrea tridentata* and *Opuntia echinocarpa* surviving a 1973 burn at Snow Creek were removed by the 1982 burn; the site is now covered by *Hymonoclea salsola* and annual grasses (*cf.*, O'Leary and Minnich, 1981).

The recent outbreak of fires, however, is clearly related to persistent above-normal precipitation and increases in native and exotic herb cover after 1976. It is important to ask whether recent burns are an aberration, and thus represent only an ephemeral event in creosote bush scrub ecology and biogeography.

Low mean annual precipitation and plant productivity at Palm Springs normally precludes short-term fire recurrences. Indeed, chaparral fires crossing the desert flanks of the San Jacinto Mountains earlier in the century stopped above desert scrub communities, owing apparently to limited fuel. Prehistoric burns doubtless extended into the desert margin on occasion when conditions were optimal. Disturbance intervals, however, were sufficiently long, perhaps centuries, to permit the establishment of long-lived desert perennials.

The western geographic limits of many taxa may thus be related to repeated, more intense burning associated with coastal sage scrub and chaparral. In southern California coastal sage scrub, burns are followed by rapid seedling establishment of *Eriogonum fasciculatum*, *Encelia farinosa*, *Salvia apiana*, *Salvia mellifera* and *Artemesia californica*, although resprouting is occasional (Malanson and O'Leary, 1982). Creosote bush scrub and coastal sage scrub are similar in that both ecosystems comprise mostly drought-deciduous mesophytic subshrubs. However, creosote bush scrub perennials, with the exception of *Salvia apiana* and *Encelia farinosa*, are poor colonizers following recurrent fire (Tratz, 1978). Indeed, recent burns have converted creosote bush scrub at Palm Springs to *Encelia farinosa* coastal sage scrub similar to stands covering semiarid interior valleys around Riverside, California.

Some desert taxa, including *Yucca schidigera*, *Simmondsia chinensis*, *Acacia greggii*, *Juniperus californica* and *Opuntia occidentalis*, extend westward into fire-prone areas of coastal southern California. These shrubs, however, are either vigorous sprouters (Tratz, 1978) or restricted to drier sites within the Pacific slope, such as at Aguanga and the Perris Plain in rain shadows of coastal ranges, and porous alluvial fans descending from the San Gabriel and San Bernardino mountains, where burning intervals are locally lengthened by low productivity (Axelrod, 1966; Smith, 1980).

The role of European exotics.—Recent burns, however, may have been encouraged by the profusion of European exotic grasses, especially *Bromus tectorum*, *B. rubens* and *Schismus barbatus*, during recent wet years. These species have continued to thrive during drier years since 1983. At Palm Springs, *B. rubens*, *Schismus barbatus* and other European grasses escape excessive summer heat through their winter annual habit. A minimum of cool-season precipitation (ca. 150 mm) appears sufficient to support these exotic grasses. In the dry interior, herbaceous cover resists decomposition resulting in accumulation of flammable fuels. Moreover, since exotic taxa may use desert habitats in ways distinct from indigenous taxa, consequent increases in herbaceous cover may thus increase fire frequencies and change the biogeography of creosote bush scrub without changes in climate.

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SUBMITTED 1 JULY 1985 ACCEPTED 18 FEBRUARY 1986

Anthropogenic Degradation of the Southern California Desert Ecosystem and Prospects for Natural Recovery and Restoration

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ABSTRACT / Large areas of the southern California desert ecosystem have been negatively affected by off-highway vehicle use, overgrazing by domestic livestock, agriculture, urbanization, construction of roads and utility corridors, air pollution, military training exercises, and other activities. Secondary contributions to degradation include the proliferation of exotic plant species and a higher frequency of anthropogenic fire. Effects of these impacts include alteration or destruction of macro- and micro-vegetation elements, establishment of annual plant communities dominated by exotic species, destruction of soil stabilizers, soil compaction, and increased erosion. Published estimates of recovery time are based on return to predisturbance levels of biomass, cover, density, community structure, or soil characteristics. Natural recovery rates depend on the nature and severity of the impact but are generally very slow. Recovery to predisturbance plant cover and biomass may take 50–300 years, while complete ecosystem recovery may require over 3000 years. Restorative intervention can be used to enhance the success and rate of recovery, but the costs are high and the probability for long-term success is low to moderate. Given the sensitivity of desert habitats to disturbance and the slow rate of natural recovery, the best management option is to limit the extent and intensity of impacts as much as possible.

> We've mined it, dammed it, irrigated it, developed it, and subjected it to nuclear assault, yet the desert, somehow both fragile and tough, manages to endure, a rugged old touchstone for us to measure ourselves against.
>
> Malcolm Jones, Jr., 1996

The landscape and native vegetation of the southern California deserts have been significantly altered during the last century by a variety of factors including: livestock grazing (Bentley 1898, Humphrey 1958), introduction of exotic species (Mooney and others 1986, Rejmánek and Randall 1994), off-road vehicle use (see reviews in Webb and Wilshire 1983), urbanization and its attendant effects (Reible and others 1982, Walsh and Hoffer 1991), and military activities (Lathrop 1983a, Prose and others 1987). Extreme temperatures, intense sun, high winds, limited moisture and the low fertility of desert soils make natural recovery of the desert very slow after disturbance (Bainbridge and Virginia 1990). Conditions suitable for plant establishment occur only infrequently and irregularly, and it may take hundreds of years for full recovery to take place without active intervention. Many of the actions of desert development and utilization have profound effects on ecosystem stability, diversity, and productivity (Rundel and Gibson 1996).

KEY WORDS: Mojave Desert; Colorado Desert; California; Human impacts; Recovery; Restoration

The literature on human impacts to the biotic and physical components of the Mojave Desert is large and diffuse. In this paper we review the major human-induced impacts on the California desert, and the prospects for natural recovery and restoration, by characterizing the effects of past actions on the Mojave Desert ecosystem and other arid lands. In addition, we briefly suggest practical strategies and methods for planning and implementing desert restoration projects and improving recovery of these areas by soil management, transplanting, direct seeding, and other techniques.

Area of Study

Our review focuses on the Mojave and Colorado Deserts of southern California, an area of approximately 10 million ha. The Mojave Desert occupies portions of Inyo, Kern, Los Angeles, Riverside, and San Bernardino counties in California. The geographical and ecological boundaries of the Mojave Desert are

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discussed in detail by Vasek and Barbour (1977) and Hickman (1993). The modern plant community of the Mojave has been characterized as ''desert scrub'' (Turner 1982, Hickman 1993), even though it is composed of several recognizable community types including: creosote bush scrub, saltbush scrub, shadscale scrub, blackbush scrub, and Joshua tree woodland (Vasek and Barbour 1977). Perennial plant diversity is low compared to the Colorado Desert: areas dominated by *Larrea tridentata* and *Ambrosia dumosa* occupy about 70% of the Mojave (Lathrop and Rowlands 1983). More than 250 species of annual plants are found in the Mojave, including 80–90 species that are endemic (Turner 1982). In Death Valley and the Salton Sink, annuals account for 42% and 47% of the local flora, respectively (Johnson and others 1978). Overall plant diversity is low below 1000 m, but increases to levels approaching more temperate habitats at higher elevations (Cody 1986).

The Colorado Desert is that part of the Sonoran Desert found mostly in Imperial and Riverside counties, California (Burk 1977). The Colorado Desert is generally separated from the Mojave Desert to the north by the Little San Bernardino, Cottonwood, and Eagle Mountains. The boundary between the two desert ecosystems is poorly defined to the east of these mountain ranges (Vasek and Barbour 1977). A bimodal rainfall pattern composed of winter frontal systems and summer convectional storms distinguishes the Colorado Desert from the western Mojave Desert (Burk 1977), where most precipitation comes from winter rains. In addition, the region is generally lower, flatter, hotter in the summer and warmer in the winter, and hosts a slightly different flora than the Mojave Desert (Hickman 1993). Dominant vegetation in the Colorado Desert is ''Sonoran creosote–bush scrub'' (Hickman 1993). Plant communities recognized by Burk (1977) include creosote bush scrub, cactus scrub, wash woodland, palm oasis, saltbush scrub, and alkali scrub. There is broad overlap of plant species between the Mojave and Colorado Deserts, but there are a significant number of freeze-sensitive arboreal species that are found only in the Colorado Desert.

Both deserts are characterized by dominant perennial plant species that are long-lived (Bowers and others 1995), some exceptionally so (Vasek 1980). Density and cover of long-lived species increases with age of the site surface (Webb and others 1987, 1988, Bowers and others 1997).

While our focus is specifically directed to the problems of desert lands in California (most of our experience is in the Colorado Desert), we believe our review will prove useful for desert management in other parts of the Southwest, northern Mexico, and in other drylands around the world.

Factors Contributing to Habitat Degradation

The following sections summarize major anthropogenic degradation factors in the southern California desert ecosystem other than agricultural development and urbanization. An understanding of the nature and the effect of disturbances is useful in estimating recovery times or determining what course of action may be required to restore a habitat. Table 1 summarizes the estimated time intervals required for affected plant communities to fully or partially recover from human-induced disturbances.

Impacts on the desert can be loosely divided into historic and current impacts. There is rarely a complete distinction between the two but, in general, the historic impacts include such things as overgrazing, aqueduct building, and the operation of the Desert Training Center in World War II. Grazing still continues, but the major impacts from grazing occurred in the mid to late 1800s. A very rough estimate of the magnitude and extent of these different activities is shown in Table 2. The following factors are not presented in order of importance.

Livestock and Grazing

Cattle and sheep have grazed almost continuously through large areas of the region from the mid-1800s to the present, although the numbers have dropped off in recent years. The establishment of ranching fostered the development of a major industry in the western United States that prospered until droughts, harsh winters, and overgrazing caused a series of dramatic herd declines in the late 1800s. Populations of sheep (60,000) and cattle (67,000) peaked in Imperial County in 1920. In 1968 there were 25,000 cattle and 138,000 sheep grazing on Bureau of Land Management (BLM) and National Monument desert lands in California, predominantly in the Mojave (Ruch 1968). In 1979, 1.8 million ha of public lands administered by the BLM in the California desert were grazed by 75,000 sheep and 14,000 cattle (Bureau of Land Management 1980). Excellent histories of grazing in the desert southwest are provided by Humphrey (1958, 1987).

No published studies have yet fully documented the impact of grazing by livestock in the California desert or estimated the time required for heavily grazed areas to recover to pregrazing levels of plant diversity, density, and cover (Oldemeyer 1994). The rarity of undisturbed reference sites and long-term studies makes it difficult to quantify the effects of grazing, but it is possible to

Table 1. Estimated natural recovery times in years for California desert plant communities subjected to various anthropogenic impacts

Impact	Location	T_{recovery}	Reference
Tank tracks (military)	eastern Mojave	65,[a] 76[b]	Lathrop (1983a)
Tent areas (military)	eastern Mojave	45,[a] 58[b]	Lathrop (1983a)
Dirt roadways (military)	eastern Mojave	112,[a] 212[b]	Lathrop (1983a)
Tent sites (military)	eastern Mojave	8–112[c]	Prose and Metzger (1985)
Tent roads (military)	eastern Mojave	57–440[c]	Prose and Metzger (1985)
Parking lots (military)	eastern Mojave	35–440[c]	Prose and Metzger (1985)
Main roads (military)	eastern Mojave	100–infinity[c]	Prose and Metzger (1985)
Military	eastern Mojave	1500–3000[d]	Prose and Metzger (1985)
Townsites	northern Mojave	80–110,[e] 20–50,[b] 1000+[f]	Webb and Newman (1982)
Pipeline	southern Mojave	centuries[g]	Vasek et al. (1975a)
Powerline	southern Mojave	33[h]	Vasek et al. (1975b)
Fire	western Colorado Desert	5[b,i]	O'Leary and Minnich (1981)
Off-road vehicle use	western Mojave	probably centuries	Webb et al. (1983)
Pipeline (berm and trench)	Mojave Desert	100[j]	Lathrop and Archbold (1980b)
Pipeline (road edge)	Mojave Desert	98[j]	Lathrop and Archbold (1980b)
Powerline pylons and road edges	Mojave Desert	100[j]	Lathrop and Archbold (1980b)
Under powerline wires	Mojave Desert	20[j]	Lathrop and Archbold (1980b)

[a] Recovery time to control density.

[b] Recovery time to control cover.

[c] Estimated recovery time for *Larrea tridentata* to reach control densities.

[d] Estimated recovery time (''if at all'') for recovery to original vegetative structure assuming establishment of control densities.

[e] Compaction recovery time.

[f] Total estimated recovery time.

[g] 30–40 years assuming linear rates of succession; 3000 years until formation of large creosote clonal rings.

[h] Incomplete recovery time in areas of high impact.

[i] Time for appearance of perennial seedlings. See Brown and Minnich (1986) in section on fire.

[j] Biomass recovery assuming that successional vegetative growth is approximated by a straight line. Recovery of long-lived species is estimated to take at least three times longer than indicated.

Table 2. Adverse impacts on California desert, their relative intensity and historical occurrence

Impact	Intensity	Current/historic
Grazing	moderate	primarily historic
Removal of native people	moderate	historic
Invasive plants	moderate/severe	historic/current
Highways	severe	current
Urbanization	severe	current
Off-road vehicles	severe	current
Agriculture	severe	both
Military operations	severe	both
Mining	locally severe	both
Linear corridors	locally severe	current

describe the nature of these impacts and their probable extent. Consequently, conclusions about the effects of grazing on arid ecosystems have been contradictory and controversial (Anonymous 1991, Borman and Johnson 1990, Coe 1990, Field 1990, General Accounting Office 1992, Gillis 1991, Poling 1991). Some argue that grazing is beneficial to rangelands, suggesting that the act of grazing stimulates new plant growth (Savory 1988). Other putative positive benefits include the dispersal of seeds, production of fertilizer in the form of excrement, and churning of soil generated by moving hooves (but see Balph and Malecheck 1985). Others point to negative impacts of grazing including: soil compaction and increased erosion, trampling of plants, and overcropping. Grazing effects on arid ecosystems are reviewed in detail by Archer and Smeins (1991).

The effects of overgrazing are far less controversial. As early as the late 1800s there was recognition of dramatic range deterioration in the United States as a result of overstocking of cattle (Bentley 1898). In his report, Bentley concluded that ''The ranges have been almost ruined, and if not renewed will soon be past all hope of permanent improvement.'' In spite of early recognition of a problem, solutions have still not been satisfactorily implemented (General Accounting Office 1992).

The impacts of grazing, whether positive or negative, may be extensive. In a recent biological assessment in the western Mojave Desert of California, 100% of a 234-square-km area was impacted to some extent by sheep grazing (Tierra Madre Consultants 1991). In a detailed analysis of the effects of sheep grazing on 2.6 square km of desert tortoise habitat, Nicholson and Humphreys (1981) observed soil disturbances in 80% of the area used by sheep. Thirty-three percent of the plot was heavily used by sheep.

Livestock grazing, by its very nature, causes a decrease in plant cover and biomass, at least initially. Decreases in cover have been shown to be associated with a decrease in the diversity and abundance of lizards and other wildlife species in arid ecosystems (Busack and Bury 1974, Germano and Hungerford 1981, Germano and others 1983, Germano and Lawhead 1986). In the Mojave Desert Nicholson and Humphreys (1981) observed large decreases in plant cover in areas grazed by sheep. Similar results were reported by Webb and Stielstra (1979) in the Mojave. In addition, they observed a 60% reduction in above-ground biomass on plots grazed by sheep. Other studies, in American deserts outside of the Mojave Desert, have not detected appreciable differences between grazed and ungrazed plots (Heske and Campbell 1991, Rice and Westoby 1978), but most sites had been grazed before the studies were initiated. An important point to make is that the response of plants to grazing varies according to species, season, plant phenology (Genin and Badan-Dangon 1991), local conditions (drought, edaphic factors, etc.), and past historical use.

Direct effects of grazing on desert animals such as the desert tortoise (*Gopherus agassizii*) are not well documented. Grazing sheep can damage tortoise burrows. Nicholson and Humphreys (1981) reported that of 164 tortoise burrows on a 2.6-square-km study site, 10% were damaged and 4% were destroyed. Most burrows were well protected since they were generally located under shrub cover. Damage was considered to be insignificant since tortoises were often observed digging new burrows in late spring regardless of the availability of existing burrows. Others have gone so far as to suggest that cattle dung actually serves as an important food supply for desert tortoises (Bostick 1990), although this has never been rigorously substantiated (Hal Avery personal communication).

Webb and Stielstra (1979) observed that soils in the Mojave Desert exhibited greater surface strength in areas where sheep bedded and grazed relative to control areas. The greatest compaction occurred in the upper 10 cm but compaction was also observed at lower depths. At the surface, soils are trampled by grazing, often obliterating cryptobiotic soil crusts leading to increased erosional potential. Erosion is of special concern for desert soils because the nutrient capital is often concentrated in the surface soil. Gross disorganization of community structure is possible with the loss of only a few centimeters of soil (Charley and Cowling 1968).

Even limited grazing can cause significant shifts in vegetation and damage to soil crusts. Kleiner and Harper (1977) found that seven plant species that were common in the ungrazed area were absent or insignificant in a comparable grazed section of Canyonlands National Park. They attributed this in part to changes in cryptobiotic soil crust, which decreased from 38% cover in the ungrazed area to 5% in the lightly grazed area. Grazing also increases the spatial and temporal heterogeneity of water, nitrogen, and other soil resources, fostering increased desertification of productive arid lands (Schlesinger and others 1990).

As stated above, the rate of natural recovery of habitats exposed to grazing depends on the intensity of past grazing and local conditions. In a blackbrush (*Coleogyne ramosissima*) association in Utah and Arizona, shrub cover is greater in areas that have never been grazed than in grazed areas. In the same area, plots protected from grazing for ten years showed no difference from heavily grazed areas indicating slow rates of recovery (Jeffries and Klopatek 1987). Exclusion of grazing for 14–19 years did not allow recovery of native perennial grasses in southeastern Arizona (Roundy and Jordan 1988). In the deserts of Kuwait land degradation does not necessarily stop following protection from grazing (Omar 1991). Drought, erosion, and sand encroachment continue to degrade land in the absence of grazing. Human activities and grazing may hasten degradation, but in concert with drought the three can be devastating.

In a recent review of the effects of grazing on public land in the hot deserts (Chihuahuan, Mojave, and Sonoran) of the American Southwest, the General Accounting Office (1992) concluded that a high environmental cost has been exacted on these fragile ecosystems and that land degradation due to grazing is continuing. The report concluded by noting that the high environmental risks, budgetary costs, low economic benefits, and management problems associated with livestock grazing on hot desert public lands merits Congressional consideration. Recommended options included raising grazing fees or appropriating additional funds to offset costs of administration and monitoring, and discontinuing livestock grazing altogether in hot desert areas.

Different plant communities respond to grazing in a variety of ways related to a complexity of factors. Results for the Mojave Desert suggest that livestock grazing can have locally significant effects on the plants (Figure 1) and ultimately on desert wildlife. Efforts to restore

Figure 1. Cattle grazing can have locally significant effects on vegetation and soils, as shown in this photo of a cattle watering area and corral in what is now the Mojave National Preserve, California. Note the almost total destruction of perennial plants in the immediate area. The visual effect is greatly diminished as distance from the watering area increases. Photo by Jeff Lovich.

degraded rangeland in the Mojave should start by considering the effects of grazing and the potential impacts of soil compaction, erosion, and plant community alteration.

Linear Corridors

Roads, railways, powerlines, and pipelines, some of the most conspicuous elements of the modern Mojave Desert landscape, are all characterized by long and relatively narrow corridors of disturbance. The fact that most linear corridors are narrow does not necessarily imply that their impacts are minimal. According to Brum and others (1983), over 8000 km of overhead power transmission lines were present in the California desert in 1980, impacting more than 28,000 ha of land. An additional 50,000 ha of land will be impacted by the year 2000 if the projected threefold increase in power demand is accurate. Information summarized in the California Desert Conservation Area Plan (Bureau of Land Management 1980) suggests that an additional 2000 km of energy production and utility corridors are needed to meet the needs of southern California to the year 2000.

The immediate effect of linear corridor construction on soil conditions and plant cover is one of nearly complete destruction (Vasek and others 1975a). In some cases recovery is retarded due to operation and maintenance of corridors (Artz 1989). Other negative secondary effects of corridors include mortality of animals along roadways (Rosen and Lowe 1994, Boarman and Sazaki 1996), habitat fragmentation and restriction of movements and gene flow, increased access to remote areas for illegal collection and vandalism of plants and animals (Nicholson 1978, Garland and Bradley 1984, Boarman and Sazaki 1996, Jennings 1991), and increased erosion (Wilshire and Prose 1987). The steel towers associated with many electrical energy transmission corridors provide nest sites and hunting perches for ravens (*Corvus corax*), a native predator that has increased dramatically in recent years due to human subsidy. The towers may allow ravens to hunt more effectively for the federally threatened desert tortoise (*Gopherus agassizii*) and other desert wildlife (Boarman 1993). Corridors can also serve as a source of exotic invasive plants brought in on construction equipment (Zink and others 1995). Invasive plants prosper in the disturbed conditions and contribute to an increased likelihood of fire. The construction of pipelines for gas, oil, and water and much more destructive than overhead lines because extensive trenching is usually required. This traditionally has led to severe soil impacts (leaving subsoil on the surface), disturbing stabilized crusts and rock surfaces, and concentrating runoff and erosion. More recent pipelines have incorporated some environmental protection and some rehabilitation but the low value of the desert land, the high cost of revegetation, and the lack of money for enforcement and supervision has often led to neglect and minimal treatment.

The impacts of linear structures can extend far beyond the boundaries of the immediate disturbance. Schlesinger and others (1989) studied the effects of diversion structures (earthen dikes) along the Colorado River Aqueduct on plants and soil. The structures were constructed to prevent runoff due to precipitation from washing sediments into open portions of the canal. Large areas downslope of the diversion structures received only incident precipitation, with essentially no runoff from the extensive drainages in the uplands above the diversion structures. As a result, large areas of desert habitat on the downslope side of the diversion structures had a lower biomass of perennial and annual plants in comparison to adjacent areas with no diversion structures.

Garland and Bradley (1984) observed that some species of rodents in the Mojave of Nevada are more abundant near highways, while others are not. However, reduced abundance may have been an artifact of natural habitat heterogeneity since no mortality was observed during the 11-month study. Another effect of roads is edge enhancement in which perennial shrubs along roadsides are denser, larger, more vigorous, and support greater numbers of foliage arthropods than those away from roadsides (Vasek and others 1975b, Lightfoot and Whitford 1991). Johnson and others (1975) noted that primary productivity, as measured by standing crop, at study sites in the Mojave Desert of California increased about 17 times on the basis of vegetated area alone and 6 times when the area of the bare road surface was included as part of the productive unit. Unpaved roads showed increases of 6 and 3 times, respectively, in each category. Increased water availability from pavement runoff and increased retention of moisture under the pavement are probably responsible for the observed increase in plant vigor, although removal of competing plants that formerly occupied the roadway may confer an advantage to plants along the berm (Vasek and others 1975a). The increase in vigor attracts herbivorous insects (Lightfoot and Whitford 1991).

The effects and recovery of linear corridor construction in deserts have been studied by several researchers. The process of natural recovery, following powerline construction in the Sonoran Desert starts immediately with invasion by pioneering annual species, but perennial species may not return for over five years. The density and diversity of annual species may increase in comparison with undisturbed sites, perhaps due to the removal of large woody species (Hessing and Johnson 1982). An effect that is apparently linked to changes in plant abundance and composition is a reduction in the density, but not the community composition, of arthropods following establishment of access roads for powerline construction (Johnson and others 1983).

In the Mojave Desert, plant cover also increases following powerline construction. The rate of increase and composition of colonizing species varies considerably, confounding the ability to predict succession relative to adjacent undisturbed areas. Ground cover of short-lived perennial species increases in areas of severe disturbance, under the central wires, and along the edge of maintenance roads. After 33 years there was a noticeable, but not complete, recovery of predisturbance vegetation (Vasek and others 1975b). Natural revegetation (0–41% ground cover) by long-lived perennials has been observed 12 years after construction of a pipeline by trenching, piling, and refilling (Vasek and others 1975a). Disturbed and control areas appear to have similar cover, biomass, and densities of vegetation following partial recovery, but similarities disappear when the proportions of long-lived and dominant species are compared (Lathrop and Archbold 1980a,b). Species with these characteristics are not well represented on disturbed sites.

Management strategies for minimizing the effects of linear corridor construction include: placement of power poles closer to existing access roads, modifying construction techniques for buried pipelines, less frequent road grading, and limiting the width of motorcycle race corridors along powerlines (Artz 1989). Lathrop and Archbold (1980b) proposed several recommendations for routing corridors to minimize environmental impacts including: (1) routing them through gently sloping areas to minimize erosion, (2) routing them through areas occupied by colonizing species such as cheesebush (*Hymenoclea salsola*), (3) avoiding areas dominated by high nitrogen fixation communities such as cat's claw acacia (*Acacia greggii*), and (4) avoidance of undue soil compaction with implementation of soil loosening efforts to aid natural revegetation. Revegetation of linear corridors was evaluated by Kay (1979, 1988), Graves and others (1978), and Brum and others (1983).

The slow recovery of the desert to linear corridor impacts is perhaps best demonstrated by the visibility of many of the old Native American trade routes. Long-term use by foot traffic alone was sufficient to compact the soil and recovery after several hundred years has not been enough to hide these trails (personal observation).

Mining

Mining has been an important activity in the California desert since the late 1880s. Mining communities such as Kokoweef, Hart Mountain, Boron, Johannesburg, and many others have had mostly localized impacts on the desert. The most obvious forms of degradation are pits, ore dumps, and tailings, but the once-great demand for fuel and timber, grazing, and road building associated with mines was unquestionably more important in the past. Fugitive dust and toxic tailings are a more recent concern from some of these mining areas.

The Bureau of Land Management (1980) estimated that 12,545 ha in the California Desert Conservation

Area had been affected by major mining operations. If the many small prospects and adits are included, the area affected by mining would certainly be larger. The brine evaporation and dry lake mine operations are extensive and lead to substantial wind erosion (Wilshire 1983). Another problem is animal mortality at poorly managed cyanide extraction gold mines in the Mojave Desert (Clark and Hothem 1991, Henny and others 1994).

Military Training Operations

Large areas of the California desert have been impacted by temporary and ongoing military activities. Major training exercises included activities by General Patton in the early 1940s, the Desert Strike operation in 1964, and Bold Eagle in 1976. Between 1942 and 1944 more than a million soldiers passed through these training facilities, which covered more than 46,800 square km (Bureau of Land Management, 1990). The camps were effectively small cities, up to 2800 ha in size (e.g., Camp Granite) (Prose and Metzger 1985). Continuing impacts are generated by active military bases including the National Training Center (at Fort Irwin, the Marine Corps Air Ground Combat Center at Twentynine Palms, China Lake Naval Air Weapons Station, and the Chocolate Mountain Aerial Gunnery Range (Lathrop 1983a). Military operations cause intensive damage in many areas but also provide protection of thousands of hectares from other sources of disturbance by prohibiting public access. At Fort Irwin alone, the area in need of remediation is estimated to exceed 50,000 ha.

The recovery of large areas of the eastern Mojave Desert subjected to military training exercises almost 36 years earlier was studied by Lathrop (1983b). Impacted areas included tent sites, roads, and tank tracks. All impacted areas exhibited significant reductions in plant density and cover relative to control areas. Reductions of cover and density were greatest in tank tracks and least in tent areas. Recovery to predisturbance levels of cover and density varied according to disturbance type. Tent areas showed the greatest recovery, and roadways showed the least, reflecting the intensity of disturbance. Recovery in tank tracks was intermediate. Diversity of dominant perennials also varied between disturbed and nondisturbed areas but results were clouded by low species richness at the study sites and small sample sizes of the subdominants. However, diversity in disturbed transects at the Camp Ibis study site was low relative to control sites. Species similarity decreased between control and disturbed transects with increased disturbance and use intensity.

Similar observations and conclusions were reached by Prose and Metzger (1985) and Prose and others (1987) at abandoned military camps in the eastern Mojave. Long-lived species such as *Larrea tridentata* were dominant in all control areas but percentage cover and density were reduced in impacted areas. Dominant plants in disturbed areas included pioneer species such as *Ambrosia dumosa* and *Hymenoclea salsola.* Percentage cover values for pioneer species in disturbed areas were equal to or greater than control values.

Differences in vegetative structure between control and impacted plots were due to soil compaction, changes in soil texture, removal of the top layer of soil, and alteration of drainage channel density (Prose and others 1987). Penetrometer measurements show that a single pass by a ‘‘medium’’ tank can increase average soil resistance values by 50% relative to adjacent untracked soil in the upper 20 cm, but values of up to 73% were recorded. Dirt roadways could not be penetrated with a penetrometer below 5–10 cm due to extreme compaction. Physical modifications to the soil beneath tank tracks extended vertically to a depth of 25 cm and outward from the track edge to 50 cm (Prose 1985).

Recovery times to predisturbance levels of density and cover were estimated by Lathrop (1983b) assuming linear rates (Table 1). Recovery to predisturbance species composition would require much longer, if it were to occur at all. Areas receiving the greatest amount of soil compaction, such as roadways, require the longest recovery times. Tank tracks and tent areas recover in a shorter amount of time. Overall, recovery in plant density is slow relative to increases in cover. In other words, the number of individuals changes little following recovery from disturbance, but surviving individuals cover larger areas. A major conclusion from Lathrop’s study was that recovery to some original level of community composition and stability may not occur in the foreseeable future. However, recovery of comparable disturbed areas has been excellent on restoration test plots at the Marine Corps Air Ground Combat Center near Twentynine Palms, California (Zink personal communication).

Off-Road Vehicles

Off-road vehicle (OHV) use is one of the major recreational activities in the deserts of California. The Motorcycle Industry Council estimated that 4.7 million motorcycles were used by 11.7 million people in 1978 for off-highway recreation in the United States, a figure that does not include dune buggies and four-wheel drive vehicles (Kockelman 1983).

The impacts of OHVs have been well documented (Webb and Wilshire 1983) and include destruction of soil stabilizers (see section on biotic components of soil), soil compaction, reduced rates of water infiltration, increased wind and water erosion, noise, decreased abundance of lizard populations (Busack and Bury 1974), and destruction of vegetation (Vollmer and others 1976). Compaction of a desert soil reduces the root growth of desert plants and makes it much harder for seedlings to survive (Bainbridge and Virginia 1990, Bainbridge and others 1995a). An excellent review of the effects of OHVs in the Mojave and other deserts is contained in Webb and Wilshire (1983) and the reader is referred to that document for information beyond that presented herein.

Soil compaction is a common effect of any compressive action on most soils. Compaction results from a variety of factors other than OHV use, including trampling by grazers, human trampling (Liddle 1991, 1997), and even raindrops (see review in Webb 1982). In the case of OHVs, compaction occurs at shallow depths related to the geometry of the contact surface between the tire and the soil interface. In one study the greatest increase in soil density occurred at a depth of 30–60 cm after being compacted by a motorcycle (Webb 1983). Soil density increases as a function of the number of vehicle passes, while soil infiltration rate decreases. Soils that are most susceptible to compaction are loamy sands and coarse gravelly soils with variable particle sizes. Wet soils are more susceptible to compaction than dry soil. Soils that are least affected include sands and clays.

Another by-product of heavy OHV use is increased wind and water erosion. The degree of erosion experienced in an area exposed to OHV use is affected by two main factors. First, increased water erosion is partially attributable to decreased infiltration rates due to compaction. Second, OHVs destroy surface stabilizers (see section on biotic components of soil), making soils more susceptible to erosion (Hinkley and others 1983). The enormity of the problem in the Mojave Desert is underscored by the fact that satellite photos revealed six dust plumes covering over 1700 square km of the western Mojave on 1 January 1973 that were attributed to surface destabilization primarily by OHVs (Nakata and others 1976, Gill 1996).

As shown in numerous photographs in Webb and Wilshire (1983), the effects of erosion can have indirect effects, since debris flows (Nakata 1983) can bury plants at some distance from the impacted area. Areas that are least susceptible to water and wind erosion following OHV use are dunes, playas, and areas with abundant coarse surface material (Gillette and Adams 1983, Hinckley and others 1983). Restoration of OHV areas affected by erosion requires actions to not only stop continuing erosion (Harding 1990, Heede 1983, Middleton 1990), but also action to restore past damage.

Desert soils vary in their susceptibility to OHV damage. Susceptibility is generally high in all areas except barren sand dunes (but see Bury and Luckenbach 1983), and the clay flats of playas. Soil damage caused by OHVs is environmentally significant due to the fact that desert soils may take 10,000 years to develop (Dregne 1983). From this estimate, Dregne concluded that it was futile to speak of disturbed soil recovery in time frames related to human occupancy.

Another major effect of OHV use is the destruction of plants. Lathrop (1983a) examined aerial photographs of nine disturbed and undisturbed areas in the Mojave Desert to assess the effects of OHV usage. Perennial plant density and cover were dramatically reduced in OHV areas. The percentage of cover and/or density in OHV-impacted areas relative to control areas was less than 15% in three of the sites examined. Destruction of plants resulted not only from crushing stems and foliage, the extensive root systems that fill the intershrub spaces, and germinating seeds, but also from the superstructure of the vehicle. The latter factor is important since it is responsible for plant destruction in an area wider than the track width of the vehicle. The wheel tracks of a full-size off-road vehicle operating in an undisturbed area can damage almost 0.5 ha of land with every 6.44 km traveled. Support vehicles, including very large and heavy motor homes, are very destructive, and camping areas are especially hard hit.

An easily detected but poorly understood effect of OHVs is noise. Noise from certain types of OHVs can reach 110 decibels, which is near the threshold of human pain. Brattstrom and Bondello (1983) demonstrated that OHV use in the Mojave Desert caused noise levels that caused hearing loss in animals such as kangaroo rats, desert iguanas, and fringe-toed lizards; interfered with the ability of kangaroo rats to detect predators such as rattlesnakes; and caused unnatural emergence of spadefoot toads that were estivating until the arrival of rain for breeding, a situation that could result in death. The authors noted that although OHVs are not the loudest source of human-generated sound in the Mojave, they occur more frequently than any other high-intensity sound source. In their report, Brattstrom and Bondello recommended that OHV areas be located away from the ranges of ''all undisturbed desert habitats, critical habitats, and all ranges of threatened, endangered, or otherwise protected desert species.''

The impact of OHV use on desert tortoises in the Mojave Desert of California was examined by Bury and Luckenbach (1986) in an unpublished report. Significantly more tortoises and active burrows were found on a 25-ha control plot than on a similar plot exposed to OHV use. In addition, subadult and adult tortoises on the control plot exhibited larger body mass than those on the OHV plot.

Impacts related to OHV use present a serious challenge to desert restoration projects for three reasons: (1) the potentially severe impact of OHV use in desert ecosystems, (2) the widespread nature of the OHV impacts in the California desert, and (3) the fact that OHV areas are often located in or near environmentally sensitive habitats. Areas targeted for restoration should be closed to OHV use prior to initiating procedures to ameliorate past damages.

Invasive Plants

Invasive exotic plants have had a significant impact on the natural communities of California (Mooney and others 1986, Rejmánek and Randall 1994), including the southern California desert ecosystem. Invasion has been facilitated by habitat disturbances that allow exotic species to colonize habitats once dominated by native species (Hunter and others 1987). Once established, exotic plants may diminish the abundance of native species due to competitive interactions or by disruption of natural processes such as fire frequency and intensity.

Some of the more important exotic plants in the southern California desert are saltcedar (*Tamarix ramosissima*), also known as tamarisk (Lovich and de Gouvenain 1998), Russian thistle (*Salsola iberica*) (Young 1991), filaree (*Erodium cicutarium*), and several grass species including split grass (*Schismus* spp.) and bromes (*Bromus* spp.) (Brown and Minnich 1986, Hunter 1991). Immense areas of desert are colonized by these species. Although other exotic plants are present in the Mojave Desert, these are important because of their ubiquity.

Exotic plants present two major problems to the integrity of the desert ecosystem. First exotic annuals increase the fuel load and frequency of fire in a community that is poorly adapted to fire. Second, some exotic plants exhibit allelopathic effects that negatively affect native species, especially annuals. Negative interactions have been demonstrated between Russian thistle and other species in the laboratory (Allen 1982a, Lodhi 1979). In addition, competition of Russian thistle with native perennial grasses increases under drought conditions (Allen 1982b), furthering establishment of the exotic. Fortunately, Russian thistle competes poorly with established vegetation and rarely supplants well-established native populations. Unfortunately, once the soil is disturbed and native plants are eliminated, Russian thistle gains a strong foothold (Young 1991). General reviews of the threats posed by exotic species invasions in native ecosystems are summarized by Cheater (1992) and D'Antonio and Dudley (1993).

Air Pollution

One of southern California's most famous exports is smog. While most noticeable in the inland valleys of the state, smog is often transported via atmospheric processes into the Mojave Desert (Pryor and Hoffer 1991). Anthropogenic pollutants include ozone, sulfur dioxide, and various particulates. Atmospheric tracer experiments have shown that pollutants released in the San Fernando Valley impact the southern Mojave Desert towns of Adelanto and Palmdale, while those released in the southern San Joaquin Valley impact the northern Mojave Desert towns of Mojave and China Lake (Reible and others 1982). Experimental tracers used in atmospheric transport studies are diluted by factors of only 2–3 during passage between source and receptor areas. Impacts are maximized during evening and nighttime hours, independent of the time of release in the San Joaquin Valley, because of the diurnal mountain–valley wind cycle. Ozone levels in the Mojave Desert can exceed 100 parts per billion (ppb) or more when offshore wind transports atmospheric pollutants from the Los Angeles Basin (Thompson and others 1984a). By comparison, ozone levels in remote areas range from 20 to 40 ppb.

The most obvious effect of smog in the Mojave Desert has been visibility degradation in an area historically distinguished by extraordinary visibility (Walsh and Hoffer 1991). Median visibility is 48–88 km in large urban areas and 104–128 km in nonurban locations. Visibility has decreased 10%–30% from the middle of the 1950s to the early 1970s at many recording stations (Trijonis 1979).

Much of the visibility loss is related to particulates, including nitrogen-rich compounds. Dryfall of these compounds from air pollution can be a major source of supplemental N for plants. This favors many exotic plant species over native annuals and perennials. Wedin and Tilman (1996) found that half the native plant species in a Minnesota grassland were lost from the community at supplemental N levels mimicking dryfall deposition rates.

A less obvious effect is damage to plants. Stolte (1991) observed injurious effects to desert plants exposed to ozone and sulfur dioxide in laboratory experiments. Annual plant species of the genera *Camissonia* and *Cryptantha* exhibit high sensitivity to both gases. The grass *Oryzopsis hymenoides* exhibits high sensitivity to sulfur dioxide, as do some types of cryptogamic soils. Responses of cryptogamic soils include increased electrolyte leakage, chlorophyll degradation, and reduced nitrogen fixation (Belnap 1991).

Studies of plants from the Mojave and Colorado Deserts show that perennial species vary in their re-

Figure 2. The effects of fire in the desert are obvious in this photo taken near Palm Springs, California, about five years after the blaze. Note the almost complete elimination of perennial shrubs in the burned area to the left. Perennial plant species in the Mojave and Colorado Deserts are long-lived and very sensitive to fire, traits that collectively contribute to the long recovery times typical of many desert plant communities after fire. Photo by Jeff Lovich.

sponse to SO_2 and NO_2. *Larrea tridentata* is sensitive to fumigation by these pollutants under experimental conditions, displaying extensive leaf injury and reduced growth or dry weight. *Encelia farinosa* and *Ambrosia dumosa* show intermediate responses, while *Atriplex canescens* appears to be resistant (Thompson and others 1980). Sensitivity also varies among native annual plants, with *Camisonia claviformis, C. hirtella,* and *Cryptantha nevadensis* exhibiting leaf injury at low concentrations of SO_2 and O_3 (Thompson and others 1984b).

Fisher (1978) suggested that high rates of mortality in desert holly (*Atriplex hymenelytra*) in the northern Mojave Desert (Death Valley) were related to elevated ozone levels. During the summer months he recorded ozone levels that were twice the national standard of 0.08 ppm. Photosynthesis and water use was significantly reduced in greenhouse experiments where seedlings were exposed to 0.15–0.18 ppm ozone for 3 h. Ozone-induced reduction in water-use efficiency was postulated to be the cause of declining *Atriplex* populations in Death Valley.

Additional summaries of the impacts of air pollution in the Mojave and Colorado Deserts are provided by Mangis and others (1991), Thompson (1995), and VanCuren (1995).

Anthropogenic Fire

Fire was not an important factor in shaping the prehistoric structure and dynamics of plant communities in the California desert. The infrequency of fire in the prehuman landscape of the desert was due to limited biomass, large intershrub spacing, low combustibility of some native plants, sparse groundcover to support and propagate combustion, and the absence of human-mediated fire suppression activities (Humphrey 1974, O'Leary and Minnich 1981, Minnich 1983, Brown and Minnich 1986). Such is not the case in other desert and semidesert areas of the American Southwest, including parts of the Sonoran and Chihuahuan deserts, where fire was an important prehistoric agent in maintaining grassland seral stages (Humphrey 1958, 1963, 1987, Reynolds and Bohning 1956).

The proliferation of exotic annual plant species such as *Bromus, Schismus,* and *Salsola* has dramatically increased the fuel load and frequency of fires in many ecosystems around the world (D'Antonio and Vitousek 1992), including parts of the California desert (O'Leary and Minnich 1981, Brown and Minnich 1986), in recent years. The frequency of fires in the Colorado Desert of California is further enhanced by the proximity of previously burned areas (Chou and others 1990). Native perennial shrubs are poorly adapted to relatively low-intensity fires as evidenced by low rates of recovery (Figure 2). In the upper Coachella Valley on the east scarp of the San Jacinto Mountains near Palm Springs, California, burned creosote bush scrub is replaced by open stands of *Encelia farinosa,* native ephemerals, and exotic species such as *Schismus* and *Bromus* (Brown and Minnich 1986).

Postfire vegetational recovery along a chaparral–desert ecotone including parts of Anza-Borrego Desert State Park in San Diego County, California was examined by Tratz and Vogl (1977). They observed high recovery (as measured by speed of resprouting) in chaparral shrubs and desert-wash plants, but low recovery in cacti. Herbivorous mammals present before the burn were also present afterwards, since rapid recovery of shrubs provided adequate food supplies for wildlife, even in the first months after the fire. If California desert perennial plant communities are not well adapted to fires, animals that coevolved in the ecosystem should not be expected to respond favorably to fire either.

According to fire personnel at the California Desert District (CDD) Office of the Bureau of Land Management (BLM), the CDD (including the Mojave and Colorado Deserts) had a ten-year average of 175 fires per year prior to 1992 (range 100–475) that affect an average of 10,927 ha annually (range 607–34,400 ha). The CDD estimates include a very small amount of BLM land outside the desert.

Impacts on Biotic Components of Soil: The Invisible Component of Biodiversity

Although emphasis is often placed on the physical and chemical properties of various soils, they contain important biotic components as well including: soil surface stabilizers such as algae and lichens, nematodes and other metazoans, various bacteria, and mycorrhizae. Odum (1994) referred to these organisms as the invisible component of biodiversity. While not as conspicuous as macrofloral elements, biotic components of soil are important symbionts that are easily destroyed by certain human activities.

Undisturbed desert areas are characterized by the presence of soil stabilizers, including lichen, fungal, bacterial, and algal crusts; desert pavement; mechanical crusts; and chemical crusts. The biotic components of these stabilizers are collectively referred to as cryptobiotic soil. Mineral-derived crusts form under a variety of physical and chemical conditions that may actually be facilitated by biotic components (Elvidge and Iverson 1983, Taylor-George and others 1983). Soil stabilizers are important agents in preventing erosion but are easily disturbed since they occur at the surface. Stabilization mechanisms include binding soil particles with thallial filaments in the case of biotic stabilizers, armoring the surface, and increasing surface roughness. Crusts also provide germination sites for vascular plants (but see Wood and others 1982), and conserve water (see review in Cole 1990). The susceptibility of crusts to damage varies according to the composition of the underlying soil. In soils subjected to large shear stresses, a single pass by a vehicle is capable of destroying well-developed crust. When the forces are mainly compressive, crusts can survive a single pass in a slightly modified form; however, OHV use is capable of quickly eliminating crusts in an impact area (Wilshire 1983).

Considerable research has been conducted on the impacts of grazing and other agents of trampling on cryptobiotic soil crusts. These crusts are very important not only because of the soil-stabilization functions mentioned above, but because they facilitate the accumulation of organic material and soil nutrients, particularly nitrogen in the upper layers of soil (Kleiner and Harper 1977, Johansen 1993), and enhance soil moisture retention (Belnap and Gardner 1993). Research in desert and semidesert areas in Utah and Arizona has consistently shown that cryptobiotic soil is heavily impacted by grazing, even light winter grazing (Kleiner and Harper 1977, Anderson and others 1982, Brotherson and others 1983). Impacts include the destruction of surface pinnacles associated with development of cryptogamic soils (Anderson and others 1982) and the virtual obliteration of biotic elements (Cole 1990). Lichens and mosses are most sensitive to disturbance, with algal components being more resilient (Brotherson and others 1983).

Cole (1990) conducted an interesting experiment at Grand Canyon National Park to examine the effect of trampling by hikers wearing lug-soled boots. Only 15 passes were required to destroy crusts. Visual evidence of biotic components was reduced to near zero after 50 passes. The results of Cole's experiment clearly illustrate the fragility of crusts to trampling.

Cryptobiotic soil recovery may require long time intervals without intervention. Following exclusion of grazing in a Utah semidesert study site, cryptobiotic cover increased from 4%–15% in 14–18 years, but only 1% per year for the next 20 years (Anderson and others 1982). Cole (1990) observed partial recovery from human trampling in one to three years and extensive recovery after five years. However, surface irregularities associated with well-developed cryptogamic cover remained low even after five years, suggesting that recovery was incomplete. Belnap (1993) noted that over 250 years may be required for full recovery on the Colorado Plateau. Recovery was improved but was still very slow when scalped experimental plots were inoculated with crusts from surrounding areas. In the northern Mojave Desert, lichen crusts may not reoccupy heavily disturbed areas even after 63 years (Wilshire 1983). Details of the formation and recovery of chemical and mechanical crusts are discussed in detail by Wilshire (1983). The nitrogen-fixation capabilities of damaged soil may take over 50 years to recover (Belnap 1995).

Important symbiotic relationships have developed between certain species of vascular plants and vesicular–arbuscular mycorrhizal (VAM) fungi and rhizobia. The small-diameter hyphae of symbiotic fungi serve as energy efficient root hairs, enabling the host plant to better absorb nutrients, particularly phosphorus (Bloss 1985) and water (Bethlenfalvay and others 1984). Rhizobia are bacteria capable of fixing atmospheric nitrogen for use by plants. The importance of VAM fungi in desert plant communities is underscored by the fact that in a recent survey of 38 plant species (19 families) in Anza-Borrego Desert State Park in the Colorado Desert of California all were colonized by VAM species (Bethlenfalvay and others 1984). Plants naturally associated with VAM that are also found in the western Mojave Desert include *Hymenoclea, Ambrosia, Opuntia,* and *Larrea.* Bloss (1985) reported numerous plant associations in the Sonoran Desert of Arizona as well.

Previous studies have demonstrated the importance of maintaining and enhancing soil microbes in restoration projects (St. John 1984, Bainbridge 1990). Establishing plants in disturbed areas with marginal soils may be difficult or impossible without the presence of a vigorous population of microbial symbionts. These symbionts are adversely affected by soil compaction. Studies have shown 1–2 m of hyphae per gram of soil in Mojave and Sonoran soils, yet virtually none in disturbed areas (Zink personal communication). Restoration is complicated by the fact that fertilizers can inhibit mycorrhizae growth.

Can the Desert Be Restored?

Plant growth and establishment are naturally slow under the extreme conditions of the desert, and disturbance makes these conditions even more severe (Bainbridge 1990). Disturbance typically reduces both the infiltration of water into the soil and the moisture-holding capacity of the soil (Bainbridge and Virginia 1990). This increases the value of rapid deep root growth, which is made more difficult by increases in soil strength from compaction and reduced soil moisture. These synergistic effects make plant establishment much more difficult after disturbance. Revegetation and restoration work can help mitigate many of these impacts and speed recovery, but the severe conditions and unpredictable rainfall still make restoration of these sites very challenging.

A brief history of revegetation studies in the deserts of California was provided by Kay and Graves (1983). Studies in the Mojave Desert are few and relatively recent. One of the earliest studies evaluated the success of revegetation efforts along the second Los Angeles Aqueduct (Kay 1979, 1988). Construction involved stripping the vegetation from an area 200 km long × 60 m between 1968 and 1970. The seeds of seven species of native plants were distributed at six 2- to 15-ha sites on the aqueduct. The seeds of all but one species, *Atriplex polycarpa,* were from local stock. Surface preparation involved ripping the soil to 25 cm on 60-cm centers to relieve compaction. A rangeland drill was used to set the seeds at a depth of about 1 cm. Success varied among plant species. *Ambrosia dumosa* exhibited good establishment on three of six sites, but only one site had numbers approaching that of adjacent undisturbed areas. *Larrea tridentata* exhibited similar results. The other species, including *Atriplex polycarpa, Ephedra nevadensis, Hymenoclea salsola,* and *Lepidospartum squamatum,* were totally unsuccessful. *Atriplex canescens* suffered as a result of heavy grazing. The most abundant shrub along the aqueduct, *Chrysothamnus nauseosus,* established itself naturally, although it was uncommon in adjacent undisturbed areas. Kay (1988) concluded that natural revegetation is good in many years and poor in others, while artificial seeding did not consistently hasten or improve plant recovery.

In another experiment along the aqueduct, Graves and others (1978) tested the effects of a single irrigation and the success of direct seeding versus transplanting. The two methods of establishment exhibited widely variable success rates from site to site and according to species, but were not enhanced by irrigation. Substrate characteristics may influence the success of irrigation as measured by the appearance of native winter annuals (Johnson and others 1978).

The overall success of the revegetation attempt along the aqueduct was low. The vast majority of the aqueduct was still a highly visible scar in the early 1980s (Kay and Graves 1983), but recovery was inhibited by grazing and OHV use. Conclusions from the study were that more attention should be focused on establishment of visually dominant species such as *Larrea tridentata,* seeding should take place as soon after disturbance as possible, areas should be protected from grazing and OHV use, and local seed stock should be utilized for all species.

Highway revegetation studies were also reviewed by Kay and Graves (1983). Survival of container-grown shrubs planted in October 1973 and February 1974 at a site in Mojave, California, was 90% in May 1974. The roots of the transplants were exposed after a heavy rain in December 1974, and all plants were dead by October 1975. *Atriplex* spp., *Chrysothamnus* spp., and *Ephedra* spp. exhibited the greatest survival. Success was limited by rabbit overgrazing and competition from Russian thistle (*Salsola*). Container plantings were more successful when planted in the late winter or early spring. Application of fertilizer encouraged both the invasion of native woody shrubs and the nonnative annual grass *Schismus arabicus.*

Others have experienced similar success in revegetation. Brum and others (1983) observed low, long-term seedling establishment for a variety of species under several irrigation treatments along a powerline transmission corridor. The overall germination–establishment rate for seedling and postseeding irrigation success was 0.3%, and 26% for transplanted seedlings. *Larrea* exhibited poor germination under field conditions and responded poorly to all revegetation attempts.

More successful revegetation has been achieved at the Nevada Test Site in the northern Mojave Desert (Romney and others 1990). Greater than 80% survival of transplanted native shrubs and grasses was achieved when plants were protected from jackrabbits and irrigation was provided periodically.

Restoration efforts in the Colorado Desert of California were reviewed by Bainbridge and Virginia (1990). Although the plant communities differ somewhat between the Colorado and Mojave Deserts, both ecosystems pose similar challenges to restoration attempts: high temperatures, intense sunlight, limited moisture availability, high levels of herbivory by rodents and rabbits, and low soil fertility. Much of the success in revegetation experiments in the Colorado Desert is due to efforts to protect plants from herbivores and the use of buried water reservoirs for irrigation. Direct seeding attempts have generally been unsuccessful relative to transplants. *Larrea tridentata,* in particular, responded well to transplanting, especially if pruned prior to planting to increase the root-to-shoot ratio.

Assessing the nature and magnitude of human-induced disturbances makes restoration planning more efficient by enabling limited resources to be directed at critical problems. Ongoing studies (Bainbridge and others 1995a,b) of the effectiveness of desert restoration techniques are steadily advancing our ability to rehabilitate degraded arid lands in the southwestern United States, and the reader is referred to these references for details beyond the brief overview given in this section.

Plant recovery usually requires container-planting activities as well as site improvement. The most common method of direct seeding is simple hand seeding, which allows species to be matched to specific site conditions, appropriate planting depths, and results in a more natural appearance than machine planting. However, limited rainfall and removal of seeds by rodents and harvester ants may severely limit seedling establishment during typical years.

Transplanting is increasingly being used to provide nurse and seed plants for the disturbed areas (Bainbridge and others 1995b). The dominant shrubs and trees of the Colorado Desert are relatively easy to grow in a nursery or maintained landscape setting, and they are well adapted to transplanting with after-care. They are more challenging to establish in the field in a low- or no-maintenance situation, although once established, growth rates can be high. Reestablishment of annuals has been more difficult. New containers and soil mixes have improved plant survival. Deep pipe and buried pot irrigation and hand watering have also been effective. Tree shelters to limit herbivory and wind damage are also important.

A full appreciation of the ecological setting and adaptation of desert plants can make establishment less costly and more successful, but it is still expensive. The cost of restoring road edge areas in Joshua Tree National Park is fairly well established (after almost 10 years of work) and runs up to $15,000 per ha to establish large potted perennials in areas that are easily accessed. The cost of duplicating this type of work at remote sites would be much higher. Research conducted by colleagues at San Diego State University has emphasized lower-cost, less-intensive restoration, but the costs (excluding research) are still on the order of $12,000–25,000/ha. Even these high project costs provide no guarantee of success.

Conclusions

Desert areas disturbed by human activities may take centuries to recover without active intervention. Undisturbed desert soils are often in a relatively stable equilibrium developed over hundreds or thousands of years. Removal of vegetation and disturbance of soil crusts or soil structure can destroy this equilibrium, leading to wind and water erosion that are very difficult or impossible to control without very high investments in material and labor.

One of the key lessons of our research in the Mojave and Sonoran deserts is the critical importance of minimizing the intensity, frequency, and area of disturbance. Past research summarized in this paper has identified the wide range of effects from human disturbance and the difficulty and the high cost of mitigating damage. While recovery rates can be increased with modest expenditures, a major restoration program to improve recovery for just the OHV-damaged areas in the California desert region could exceed one billion dollars. Available funding will permit only a limited restoration for selected sites, even with continuing generous contributions of volunteer labor. Fences, signs, and enforcement to prevent further damage may often be a better investment than intensive restoration.

Recent research in the Mojave Desert demonstrates the benefits that protection can impart, even to previously disturbed areas. Brooks (1995) conducted a comparison between the Desert Tortoise Research Natural Area (DTNA) and unprotected land immediately adjacent. The DTNA was fenced to prohibit both OHV use and sheep grazing between 1978 and 1979. By the time of his study in 1990–1992, Brooks demonstrated that aboveground live annual biomass was generally greater inside than outside the fenced area, with the exception that the exotic annual grass *Schismus barbatus* produced more biomass outside the fenced area. Percent cover of perennial shrubs, seed biomass, and rodent density and diversity were also greater inside the fenced area.

To be successful, revegetation and restoration require careful attention to ecological relationships, both above and below ground, herbivory, soil characteristics, microclimate, and patterns of moisture availability (Bainbridge 1990, Bainbridge and others 1995a). Undoing the damage done to the soil system by disturbance is a critical step toward recovery and restoration. In general, strategies that recreate or mimic natural conditions are most likely to speed recovery of the entire ecosystem.

Research conducted in the Mojave and Colorado desert ecosystem has important applications for the American Southwest and throughout the world's arid zones. These areas have deteriorated rapidly under pressure from overgrazing, poor farming, and removal of trees and shrubs for fuelwood. The lessons learned in the desert ecosystem of southern California may help people living in these areas to protect or restore the productivity of their lands, and improve their lives.

Acknowledgments

We gratefully acknowledge the following people for their assistance and comments during the preparation of this manuscript: Hal Avery, Kristin Berry, Bill Boarman, David Cole, Richard Franklin, June Latting, Michael Liddle, Mike Mitchell, and Howard Wilshire. Research was supported by a grant from the California Department of Parks and Recreation, Off-Highway Motor Vehicle Recreation Division. This paper is dedicated to the memory of June Latting.

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via electronic and US mail per service list attached

July 8, 2009

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RE: Application for Certification for the Ivanpah Solar Electric Generating System Docket No. 07-AFC-5: Comments on Staff Report for the Preliminary Staff Assessment December 2008 (07-AFC-5) CEC-700-2008-013-PSA – Ivanpah Solar Electric Generating System and the Draft Desert Tortoise Translocation/Relocation Plan

Dear Mr. Kessler,

The Center for Biological Diversity ("Center") is a non-profit environmental organization dedicated to the protection of native species and their habitats through science, policy, and environmental law. The Center has over 60,000 members throughout California and the western United States, including members that live nearby the vicinity of the proposed Ivanpah Solar Electric Generating System (ISEGS) and recreate there. On July 2, 2009, the Center was granted leave to intervene in this proceeding. The Center submits these comments regarding the December 2008 Staff Report for the Preliminary Staff Assessment ("PSA") and the Draft Desert Tortoise Translocation/Relocation Plan on behalf of our board, staff and members.

I. INTRODUCTION

The development of renewable energy is a critical component of efforts to reduce greenhouse gas emissions, avoid the worst consequences of global warming, and to assist California in meeting emission reductions set by AB 32 and Executive Order S-03-05. The Center strongly supports the development of renewable energy production, and the generation of electricity from solar power, in particular. However, like any project, proposed solar power projects should be thoughtfully planned to minimize impacts to the environment. In particular, renewable energy projects should avoid impacts to sensitive species and habitat, and should be sited in proximity to the areas of electricity end-use in order to reduce the need for extensive new transmission corridors and the efficiency loss associated with extended energy transmission. Only by

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maintaining the highest environmental standards with regard to local impacts, and effects on species and habitat, can renewable energy production be truly sustainable.

The current site proposed for this project in the Ivanpah Valley is relatively devoid of human disturbance except for a few dirt roads and the existing Southern California Edison (SCE) transmission lines and associated structures. We concur with the Preliminary Staff Assessment which states, "The ISEGS project would have major impacts to the biological resources of the Ivanpah Valley, significantly affecting many sensitive plant and wildlife species and eliminating a broad expanse of relatively undisturbed Mojave Desert habitat." PSA at pg.1-9.

Significant impacts have been identified for a suite of species (PSA pg 5.2-1), including the federally and state listed threatened desert tortoise, and rare plants including Rusby's desert-mallow, cave evening-primrose, Mojave milkweed, and desert pincushion, and negative impacts to numerous other rare plants and animals. Additionally, over 2000 ephemeral drainages covering 198 acres of waters of the state would be impacted by the ISEGS on the proposed site. The following comments address those issues:

II. COMMENTS ON THE DECEMBER 2008 PSA AND DRAFT TORTOISE RELOCATION PLAN

A. The Alternatives Analysis Outlined in the PSA Fails to Comply with CEQA or NEPA

Pursuant to CEQA, the "policy of the state" is that projects with significant environmental impacts may not be approved "if there are feasible alternatives or feasible mitigation measures available which would substantially lessen the significant environmental effects…" Pub. Res. Code § 21002; CEQA Guidelines § 15021(a)(2). A Project should not be approved if environmentally superior alternatives exist "even if these alternatives would impede to some degree the attainment of the project objectives, or would be more costly." CEQA Guidelines §§ 15021(a)(2), 15126.6; Pub. Res. Code § 21002. The Project must be rejected if an alternative available for consideration would accomplish "most [not all] of the basic objectives of the project and could avoid or substantially lessen one or more of the significant effects." CEQA Guidelines § 15126.6(c).

Accordingly, the environmental review documents must consider a range of alternatives that would achieve the basic objectives of the project while avoiding or substantially lessening significant environmental effects, and it is essential that the "EIR shall include sufficient information about each alternative to allow meaningful evaluation, analysis, and comparison with the proposed project." CEQA Guidelines § 15126.6(d). Alternative sites must also be considered where relocating the project would substantially lessen the significant impacts of the project. Guidelines Section 15126.6(f)(2). *See Citizens of Goleta Valley v County of Santa Barbara* (1988) 197 Cal.App.3d 1167, 1178; *Save Round Valley Alliance v. County of Inyo* (2007) 157 Cal.App.4th 1437, 1456 (whether an alternative site may be feasible even where it requires a change in land use designation; to determine feasibility requires detailed analysis of the alternatives; and even if an alternative is less profitable than the project as proposed it may still be a feasible alternative).

NEPA similarly requires that a range of meaningful alternatives be explored in the environmental review process. 42 U.S.C. §§ 4332(C)(iii),(E). The agency must "study, develop, and describe appropriate alternatives to recommend courses of action in any proposal which involves unresolved conflicts concerning alternative uses of available resources." 42 U.S.C. § 4332(2)(E). This requirement applies whether the agency undertakes an environmental assessment ("EA") or an environmental impact statement ("EIS"). 42 U.S.C. § 4332(2)(E); *see* 40 C.F.R. §§ 1501.2(c), 1508.9(b). In addition, pursuant to the BLM's CDCA plan, impacts to wildlife from conflicting land uses should be avoided. CDCA Plan at 28. Impacts to BLM sensitive plant species, such as the Rusby's desert mallow, should also be avoided. CDCA Plan at 37. Avoidance can best be accomplished through alternative project siting and/or project design.

Most importantly in this instance, the EIR/EIS must look at alternative sites that could avoid impacts to desert tortoises and essential desert tortoise habitat, and which would avoid any need to move the tortoises off their native habitat – a so-called mitigation measure that in practice has proved to be a disaster for the species. The EIR/EIS should also fully explore other alternatives that would achieve the same level of renewable energy production—the basic objective of the project—but without the significant impacts of the proposed project.

While the PSA provides some review of alternative sites, we do not believe that the agency has as yet adequately explored alternative sites. This is evidenced by the fact that both alternative sites that were discussed in any detail—Siberia East Alternative and Broadwell Lake—would have similar impacts to biological resources as the proposed project. PSA at 7-2. Simply looking at sites with similar impacts as the proposed project does nothing to fulfill the agency's duty under CEQA. It strains credulity to believe that there are no other sites in California where the valid project objectives could be accomplished without lessening the significant impacts. Alternatives sites on previously disturbed lands, for example, should be explored including areas that were previously heavily disturbed for farming that has since been abandoned or reclaimed and un-reclaimed mining sites in the California desert. In addition, the Sierra Club recently proposed that an alternative site within the Ivanpah Valley closer to the highway be considered. To the extent that such an alternative site may limit some impacts it should also be explored as part of a meaningful range of alternatives. The agency is charged with considering alternatives to avoid and minimize impacts, it cannot lawfully fulfill this duty based on the limited alternatives analysis presented in the PSA.

In addition, by limiting the alternatives sites evaluated in detail in the PSA to sites on BLM lands with pending applications from this same project applicant (PSA at 7-9), the PSA fails to consider all feasible alternatives. Also of particular concern is the PSA's rejection of all alternatives sites on private lands that have previously been disturbed and which would therefore avoid many of the significant biological impacts of the proposed project. These alternatives were eliminated not because they are infeasible but because they would be "challenging." PSA at 7-65. This is unacceptable. The PSA analysis is deficient because it failed to meet the requirements of CEQA as outlined in *Preservation Action Council v City of San Jose* (2006) 141 Cal. App. 4th 1336. In *Preservation Action Council*, the Respondent lead agency relied heavily on the Real Parties' project objectives and the EIR rejected a smaller alternative that would have met all project objectives except for size, and would have been environmentally superior. *Id.* at 1355. The Court rejected the EIR finding that it did not meet the information requirements of CEQA because the inadequacies in the EIR's analysis "meant that the public and the City Council were not properly informed of the requisite facts that would permit them to evaluate the feasibility of this alternative." *Id*. The PSA draft provided to date is similarly deficient.

The PSA provides a basic description of the objectives of the project (PSA at 7-6 to 7-7), but it then unreasonably narrows the objectives used to consider the viability of alternatives and unreasonably includes timing of the environmental review as a basic objective of the project. PSA at 7-7. Given that the staff has stated that the applicant has to date failed to complete necessary studies and provide other information needed for the environmental review (*see, e.g.*, Status Report #7 filed March 4, 2009, at 1, 4-5; *see also* PSA at 5.9-11 (applicant has not provided information on water needs), the timing of the environmental review cannot fairly be used as a "basic objective" of the project such that it limits the consideration and evaluation of alternatives that would avoid significant impacts to environmental resources of California. Indeed, to the contrary, it appears from the available documents filed to date that the applicant has thus far been unable to provide the complete surveys and information regarding the impacts to the desert tortoise, which indicates that this site may be inappropriate for such a large-scale industrial development project. This further underscores the need for the agency to comprehensively explore a range of alternative sites that will avoid these and other significant impacts of the project.

Similarly, including "high solarity" and ground slope as basic objectives of the project (PSA at 7-7) provides an overly narrow view of the alternatives of the project. The basic objectives of the project are to provide 400-MW of renewable power in California. This goal can be met in a number of ways by feasible alternatives that would avoid impacts to the desert tortoise and intact habitat, rare plants, water resources, and waters of the state. While "high solarity" may be necessary for the type of large-scale solar thermal plant that the applicant prefers to build, the added costs and energy losses from transmission may make it more cost effective to locate a solar power generating facility closer to the point of use in the cities such as Los Angeles and San Diego which have significant "solarity" even if it is not the very highest amount. In evaluating this factor the agency should assess whether re-use of disturbed sites near existing population centers could both meet the project objectives and avoid many of the significant environmental impacts of the project including impacts to rare and endangered species. Given the economic set-backs in the past year, there are more and more large-scale industrial areas that are under-utilized in many parts of southern and central California. These industrial parks, malls and auto rows long ago replaced native habitat, they are connected to the power grid, and are readily accessible to workers. Converting these areas to solar centers is a feasible alternative that would have many societal benefits (including maintaining robust economic zones and avoiding urban blight) and would avoid nearly all of the environmental impacts of siting this project in intact desert tortoise habitat in the Mojave desert. Accordingly, the EIR should also explore the use of distributed smaller-scale solar as an alternative.

B. Additional Analysis is Needed to Assess All Impacts that Require Avoidance and Minimization

Even if the Project is eventually approved to go forward at the Ivanpah site, significant impacts must be avoided to the extent feasible and minimized. Some impacts that were not fully analyzed in the PSA that will need to be avoided or minimized and mitigated include growth-inducing impacts, fire risk, and habitat fragmentation.

Growth-Inducing Impacts: CEQA requires environmental analysis to consider the ways in which the proposed project could foster economic, housing, or population growth, whether directly or indirectly in the surrounding environment. Guidelines § 15126.2(d); *see also* 14 Cal. Code Regs § 15358(a)(1) ("Indirect or secondary effects may include growth-inducing effects and other effects related to induced changes in the pattern of land use, population density, or growth rate, and related effects on air and water and other natural systems, including ecosystems."). The Guidelines specifically require that the EIR should "discuss the charateristics of [] projects which may encourage and facilitate other activities that could significantly affect the environment, either individually or cumulatively." Guidelines § 15126.2(d). Growth-inducing impacts from the proposed project in the Ivanpah Valley include encouraging additional large-scale solar projects to be sited in this same area and making it more likely that additional solar development projects could be approved in this same area. For example, the placement of one industrial project with a new powerline connection, substations, and/or new access roads may make it more likely that a second or third project will be sited in this area. Siting multiple projects in this area could lead to complete collapse of the habitat values in this valley due to habitat loss and fragmentation. This would be a significant change to an area which now contains a significant amount of contiguous, high value, intact habitat for the desert tortoise and other species. The need for additional analysis of the impacts from multiple solar projects that have pending applications in this area is discussed further below in the section on cumulative impacts.

Fire Risk: Because the ISEGS project is a solar concentrating thermal power plant, which is comprised of fields of heliostat mirrors focusing solar energy on boilers located on centralized power towers, the superheated fluids that are essential for the operation of the project will be primarily sequestered in and adjacent to the power towers/generation site. The superheated liquids are a fire threat, particularly if flammable materials, like vegetation, are located nearby. With the majority of the site comprised of heliostat mirrors, which only reflect and focus the sun's ray on the power tower and do not contain any superheated liquids, there may be opportunities to conserve some of the existing on-site vegetation and habitat, which would avoid and minimize the impacts to the existing biological resources. In fact, solar farms are including habitat features into their project design http://www.optisolarfarms.ca/sarnia.htm. This same type of solar technology already installed and producing solar energy in Spain includes vegetation between the mirrors http://www.solarpaces.org/Tasks/Task1/PS10.HTM . Despite the problems of habitat fragmentation, vegetation islands provide stepping stones for wildlife across the site and are an improvement over complete vegetation removal.

Potential Minimization by Preservation of Vegetation: One of the maintenance issues with the heliostat mirrors is dust deposition resulting in decreased efficiency. Maintaining native vegetation will help to keep the fragile soils in place on the project site, reducing the amount of soil particles that could get airborne and be deposited on the mirrors. This will in turn reduce the need for groundwater pumping to provide water to wash the mirrors. Leaving vegetation in place provides the additional benefit of not increasing the particulate matter (PM) in the already compromised Mojave Desert Air Quality Management District.

We urge CEC staff to more fully explore the benefits of maintaining vegetation and habitat on site for this proposed project in the Final Staff Assessment.

C. Desert Tortoise: Analysis of Impacts is Inadequate and the Translocation Plan is Unsupportable

The desert tortoise is continuing to decline throughout its range (USFWS 2008) despite being under federal and state Endangered Species Acts protection as threatened. Prior to 2002, the project area was designated by BLM as Category 1 habitat for desert tortoise – the best desert tortoise habitat. The Northern and Eastern Mojave Plan (BLM 2002) changed that designation, not based on any site specific science, but on the establishment of Desert Wildlife Management Areas (DWMA's) elsewhere.

New science has become available since our scoping comments for the federal process (CBD scoping comment letter dated November 30, 2007). Murphy et al. (2007) undertook extensive genetic analysis across the range of the desert tortoise and identified genetically unique populations within the larger listed population. The desert tortoise located on the Ivanpah site represent a unique genetic group – the northeastern Mojave group. This localized area around the Ivanpah area is the only location of this unique genotype in California. Because these animals represent such a unique occurrence in California, adequate avoidance, minimization and mitigation must be applied to this project. The uniqueness of this population is also recognized both in the 1994 Desert Tortoise Recovery Plan (USFWS 1994) and the draft Revised Recovery Plan (USFWS 2008) as the North Eastern Mojave Recovery Unit and the Murphy et al. paper only confirms the uniqueness of this population.

Additionally, the Scientific Advisory Committee of the U.S. Fish and Wildlife Service's Desert Tortoise Recovery Office has recently concluded that "translocation is fraught with long-term uncertainties, notwithstanding recent research showing short-term successes, and should not be considered lightly as a management option. When considered, translocation should be part of a strategic population augmentation program, targeted toward depleted populations in areas containing "good" habitat. The SAC recognizes that quantitative measures of habitat quality relative to desert tortoise demographics or population status currently do not exist, and a specific measure of "depleted" (e.g., ratio of dead to live tortoises in surveys of the potential translocation area) was not identified. Augmentations may also be useful to increase less depleted populations if the goal is to obtain a better demographic structure for long-term population persistence. Therefore, any translocations should be accompanied by specific monitoring or research to study the effectiveness or success of the translocation relative to changes in land use, management, or environmental condition." (SAC 2009). Translocation should be used as a tool to augment populations within depleted recovery units, not as a mitigation strategy to allow for development in desert tortoise habitat.

The project fails to evaluate as an alternative or as an avoidance measure moving the project site from its proposed location to the proposed desert tortoise relocation areas, which are identified in the *Draft Desert Tortoise Translocation/Relocation Plan*. Note is made in translocation/relocation plan, that the area adjacent to Interstate 15 already has a lower population of desert tortoise, therefore impacts to the species would be reduced, the cost of implementation of any translocation/relocation that would need to be done, and tortoises that would have to be moved, would be moved into habitat that should be less affected by global climate change. Selecting a better site for project implementation that avoids, and minimizes the impacts to the environment is required under CEQA.

Draft Desert Tortoise Translocation/Relocation Plan for the Ivanpah Solar Electric Generating System: As noted in the PSA, at least 25 desert tortoises currently utilize the site. Translocation is proposed as the primary methodology for minimizing and mitigating impacts to these animals but the costs of such a project in terms of monetary outlays for the translocation, short and long term monitoring and surveys, are not discussed in the PSA. More importantly, the cost to the species of the translocation is not addressed in the PSA. For example, translocation is documented *at best* to have an 80% maximum success rate on small scale translocations (Dodd and Siegel 1991, Field et al. 2007). Indeed, the recent translocation project at Fort Irwin has already documented over 22% mortality *in the very first year* with 147 confirmed deaths out of 647 tortoises moved.

If translocation is approved for use as in this instance, the agency should carefully review the Desert Tortoise Recovery Plan (USFWS 1994) which provides seven recommendations for translocating desert tortoises. While the guidelines from the 1994 Recovery Plan are included in the Draft Translocation/Relocation Plan as Appendix B, several of these guidelines are not implemented within the Draft Translocation/Relocation Plan. Not only does the Draft Translocation/Relocation Plan fail to implement the recommendation in the Recovery Plan, it also fails to implement the Guidelines For Clearance And Translocation Of Desert Tortoise From The Ivanpah Solar Electric Generating System (ISEGS) Project dated 12/12/2008, which is U.S. Fish and Wildlife Service's guidelines included in Appendix A.

With regards to the Desert Tortoise Recovery Plan (1994) the project fails to include the following:

- Recommendation #2. The Draft Translocation/Relocation Plan fails to implement adequate monitoring to in fact, confirm that desert tortoise "establish home ranges and

- Recommendation #3. At least temporary fencing should be included in the relocation areas as well, due to the well documented fact that desert tortoises will try to return to their home range. Additionally, no provisions to deal with the fact that desert tortoises will end up along the new tortoise proof fences of the project site, trying to get back to their home territory, are included in the Draft Translocation/Relocation Plan. This behavior leaves them vulnerable to predation, and needs to be addressed.
- Recommendation #5. While FWS indicates that the density of desert tortoise should not exceed 39 animals/square kilometer, according to their guidelines, that is based on the Fort Irwin translocation, which has had a higher than normal death rate. Also, Fort Irwin is within a different Recovery Unit than the ISEGs project. Because significant numbers of carapaces were also identified on site, it may be more appropriate to determine the historic carrying capacity based on estimates of the carapaces and live animals. This number would more realistically reflect the recent carrying capacity of the landscape for desert tortoise. Additionally, in light of global climate change and the predicted warming of the desert, translocation zones should only be located at *higher* elevations, not lower parts of the Ivanpah Valley.
- Recommendation #6. The "latest available technology" to determine desert tortoise health for Upper Respiratory Tract Disease (URTD) is the Eliza test for the mycoplasmas. However, the Draft Translocation/Relocation Plan only proposes looking for symptomatic signs of infection. The Fort Irwin translocation required that all desert tortoise to be translocated be checked for exposure to disease, and those that tested positive were removed from the population in order to prevent disease spread. In addition, the host population was also tested for disease. In order to prevent an epidemic outbreak of disease, unhealthy animals should not be moved into healthy populations nor should healthy animals be moved into unhealthy populations, yet the Draft Translocation/Relocation Plan fails to acknowledge or test for this simple epidemiological issue. Translocation concentrates desert tortoise into higher densities, where diseases could be more problematic. Therefore identification of diseased animals and minimizing outbreaks of disease needs to be more fully addressed in the Draft Translocation/Relocation Plan.
- Recommendation #7. A two-year study should be undertaken on the host population, which the Draft Translocation/Relocation Plan fails to include.

On page 3 of the document, the applicant fails to incorporate the basic requirements put forth in Appendix A from U.S. Fish and Wildlife Service, which state that desert tortoise proof fencing will be necessary along I-15 and must be provided by the applicant. However in the Draft Translocation/Relocation Plan, the applicant suggests that CalTrans may be the entity putting in desert tortoise fencing. Relying on CalTrans' mitigation, presumably for the Joint Port of Entry project, fails to relieve the project applicant of their mitigation responsibilities for impacts to a federally and state listed threatened species. Additional adequate mitigation must be identified.

Under Transporation and Release, the Draft Translocation/Relocation Plan proposes that "Relocated tortoises would not be placed in existing occupied burrows" (at pg. 4). Desert tortoise generally have multiple burrows within their home ranges, which could all be considered to be "occupied", even if the animal is not always present (Luckenbach 1984). Greater clarification needs to be included on how the translocated tortoises will be kept from using on-site burrows, based on the fact that they will be moved into existing home ranges of other tortoises.

In that same section (at pg. 5), reporting is to be provided to the BLM. In addition, the U.S. Fish and Wildlife Service and the California Department of Fish and Game also need to have these reports submitted to them as the permitting agencies.

The Draft Translocation/Relocation Plan fails address all potential predators, and focuses almost exclusively on ravens. Ravens predate primarily on young tortoises, while the high level of mortality from the Fort Irwin translocation came from canids. A more comprehensive anti-predation strategy needs to be included.

In accordance with the guidelines provided by U.S. Fish and Wildlife Service (in Appendix A), "Brightsource must perform all clearance survey and translocation procedures for any portion of the project site during the spring (i.e., March-May) or fall (i.e., late August to early October) to avoid extreme temperatures". In other words tortoises should not be moved during the winter as proposed in the Draft Translocation/Relocation Plan on page 5.

Because translocation/relocation is still an experimental procedure, the proposed monitoring is inadequate to fully evaluate the even the short-term success of the desert tortoise translocation/relocation, and falls short of the guidelines that U.S. Fish and Wildlife Service provide in Appendix A. Three years of monitoring is inadequate to evaluate if the tortoises have successfully established home ranges, much less integrated into the social structure of the existing population. The goal as established in the Recovery Plan (1994) is to have the translocated/relocated tortoises integrated into the population *reproductively*, so that genetically, they continue to add to the diversity of the species. Three year of monitoring is wholly inadequate to evaluate if the tortoises have achieved this essential success criteria. We recommend that a minimum of fifteen years of monitoring of the translocated/relocated and host tortoises be required, or until unequivocal proof is acquired that shows reproductive success between the host and translocated/relocated populations (desert tortoise females can store sperm in excess of two years – Palmer et al. 1998)

Karl (2007) applied an intensive and thoughtful small-scale translocation effort, which included mapping all tortoise home ranges of both the translocated and host populations prior to translocation. Translocated tortoises were moved onto a site where their home ranges were mimicked as much as possible, including construction of burrows at appropriate locations, moving "neighborhoods" of tortoises in-tact so that the translocated animals would run into their known neighbors, fencing the translocation site, canid abatement, etc.

If habitat is left on site, as described in the avoidance and minimization section above, the EIR should also explore whether some tortoises could be left on site in the remaining habitat. Desert tortoises are known to successfully survive and reproduce in industrially altered landscapes (Lovich and Daniels 2000). Clearly, a comprehensive program on desert tortoise avoidance would also need to be developed and implemented if they were to be retained on-site, and that program needs to be included as part of the CEQA process.

In addition to the avoidance and minimization measures and translocation efforts, adequate mitigation at a rate of at least 5:1 to off-set the impacts to the desert tortoise is required, including acquisition of private lands in nearby desert tortoise habitat to be set aside as tortoise conservation areas. In order to accurately mitigate for the desert tortoise population that will be affected by the proposed project, the mitigation needs to occur within this same recovery unit, and as close to the proposed project site as possible. Additions to/expansions of the existing DWMA's and in other areas where a higher level of conservation for desert tortoise needs to put in place (ie. conservation as the highest priority), may also be a mechanism for required mitigation. Additions to/expansions of the Mojave National Preserve may also be appropriate.

D. Bighorn Sheep: Analysis of Impacts is Incomplete

Important native (i.e. not re-introduced) populations of desert bighorn sheep occur in the Clark, Mesquite and Spring mountains (Epps et al. 2004) adjacent to the ISEGS. Bighorn are a large and wide-ranging species that require connectivity across large landscapes in order to assure persistence. Existing anthropogenic barriers have already eliminated gene flow between certain populations (Epps et al. 2005). Elimination of sheep connectivity by ISEGS could lead to further isolation and inbreeding issues. Additional information on bighorn sheep movement corridors and the impact of development on them needs to be included. Avoidance of these areas needs to be included, or minimization and effective mitigation if the project actually could impact these important linkages.

Furthermore, no studies have been done on the effects that miles of mirrors may have on bighorn sheep movement or effects of their use of historical lambing areas. Data indicate that human caused disturbance negatively affects species fitness and population dynamics via the energetic and lost opportunity costs of risk avoidance (Frid and Dill 2002). More information about the potential impact from the installation and operation of mirrors on desert bighorn needs to be included.

Lastly, desert bighorn rely on springs and seeps, especially during the harsh summer months for their survival in the ranges adjacent to the proposed project site. Please refer to our water resources section pertaining to impacts to seeps and springs from the groundwater pumping proposed by the project, and please provide an analysis of the potential impacts to bighorn sheep.

E. Rare Plants: Analysis of Impacts and Avoidance Measures is Incomplete

As stated above, avoidance is the most preferred method to eliminate impacts to rare plants. Incorporation of design elements that would avoid rare plants should be fully investigated in the Final Staff Assessment, particularly for those species that are proposed to be significantly impacted including the Rusby's desert mallow (*Spheralcea rusbyi* var. *eremicola*), Cave evening primrose (*Oenothera cavernae*), Mojave milkweed (*Asclepias nyctaginifolia*), and Desert pincushion (*Coryphantha chlorantha*). Eleven additional rare plant species will also be impacted with 2-30% of their known populations proposed to be eliminated through project construction. The proposed site is also dense with cacti including approximately 6,400 barrel cactus.

Transplantation of rare plants has been documented to be mostly unsuccessful. Feidler (1991) found that mitigation-related transplantation, relocation and reintroduction projects involving endangered and threatened and rare plants was successful only 15% of the time. Reseeding of *Spheralcea rusbyi* var. *eremicola* (and other species) has occurred as part of on-site mitigation in the past (Hiatt et al. 1995) and met with at least short-term success (no monitoring was required by the project, but the authors voluntarily monitored for two years). Success for reestablishment was predicated numerous factors and were taxon specific.

Cacti have been successfully salvaged and replanted and that strategy where appropriate should be considered either on/off site.

If relocation is to be part of the mitigation effort, then a clear and concise relocation plan should be developed and included as supporting documentation in the Final Staff Assessment for public review. So many times these plans are proposed to be developed in the future, with no public input or review. We believe these plans should be included as part of the CEQA process and that their absence is a violation of CEQA. If plants are to be moved, requirements for interim monitoring during establishment (including triggers for adaptive management to meet the needs of plant survival) need to be put in place. Long-term monitoring for survivorship and successful reproduction and establishment also needs to be included as part of the mitigation requirements if relocation is a chosen strategy.

To assure conservation of the rare plants in addition to avoidance and minimization and mitigation presented above, seed collection and curation into a seed bank should be required, to preclude potential genetic loss of the species if the mitigation measures should fail.

If avoidance is not possible, then securing additional sites for conservation in perpetuity will be necessary. Focused surveys for locations outside of the project impact "footprint" must be done, and mechanisms must be put in place to secure those areas from future impacts. Actions such as eliminating grazing, establishing an extension to the DWMA in conjunction with higher levels of conservation, or an annexation into the Mojave National Preserve should all be reviewed.

F. Water Resources: Requires Additional Information and Analysis

Section 5.9 indicates that 76 to 149 AFY of water will be used to wash the mirrors and other site specific activities. Although no water will leave the site, additional information on the effects of groundwater pumping on nearby seeps and springs in the adjacent mountains. No data is presented that addresses the hydrological connection between these essential wildlife sustaining locations and the proposed project impacts.

Additionally, because of the substantial evaporation rate at the project site, please provide data on how much pumped ground water will actually be returned to the groundwater basin.

Waters of the State: The PSA indicates that 198.72 acres of Waters of the State, which include 1,973 ephemeral washes with a cumulative length of 291 miles of channels will need to be mitigated. Again we urge the CEC to look at avoidance and minimization of the impact through alternative siting.

If this site is ultimately approved for the project, because of the topography, water will still flow through the site. The project design must include measures to route water to minimize potential damage to the proposed infrastructure, while still allowing flow through to Ivanpah Lake, and supporting desert wash habitat. For example, the proposed configuration of the three solar sites should be revised to accommodate washes in the design stage.

As with the other sensitive resources, securing additional sites for conservation in perpetuity will be necessary, and may be accomplished in conjunction with sensitive species mitigations. Because the proposed project is relying on groundwater pumping as its water source, it is crucial to replicate the existing surface hydrology to enable groundwater replenishment, particularly with regards to the slow pace of groundwater recharge in the desert.

G. Cumulative Impacts are Not Fully Disclosed and Analyzed

Even before undertaking a fully adequate analysis of the cumulative impacts as outlined in the Cumulative Scenario, the PSA admits that there will be significant cumulative impacts from this project and concludes simply that there should be additional mitigation. PSA at 1-10. However, CEQA requires not only full disclosure of cumulative impacts but a full and fair effort on the part of the agency to first avoid such impacts, and then to ensure any remaining impacts are minimized and mitigated. Until the agency completes an adequate alternatives analysis, the staff conclusions that not all cumulative impacts can be mitigated are premature.

The cumulative impacts section needs to be updated to include more specific information regarding the Desert Xpress high-speed rail project. The Desert Xpress Draft Environmental Impact Report has been out for public review and presumably is moving towards finalization. One of the two proposed alternatives includes the ISEGS project site. Clearly there will be more impacts to the proposed desert tortoise relocation areas and potentially the translocation areas, if this alternative is selected.

Additionally, the cumulative impacts need to identify the impacts to desert tortoise by translocation and relocation efforts. As the other potential projects get implemented, it will push higher and higher numbers of desert tortoises into smaller and smaller areas. As proposed in the Draft Translocation/Relocation Plan, the translocation areas proposed for the ISEGs project will be effectively isolated if the Desert Xpress alternative is implemented. It will be surrounded by impermeable projects including the I-15 interstate to the east/south, the golf course to the north, the ISEGS to the north and west and the railway to the west, and therefore provides inadequate mitigation for the long-term survival of the species in this area. Additional development of other renewable energy projects in the northern part of the Ivanpah valley will also further isolate the existing population of resident, relocated and translocated desert tortoise in the northern and eastern recovery unit, even if the train proposal is not implemented in this area.

These same potential isolation issues due to the cumulative impacts of projects proposed in the Ivanpah Valley also need to be discussed for desert bighorn sheep. All of these cumulative impacts need to be included and analyzed in the final staff report.

III. CONCLUSION

For this and future proposed projects, mechanisms should be put in place that encourage solar facilities to be proposed and sited on disturbed lands instead of in fully ecologically functioning habitat such as is found in the Ivanpah Valley, which support a variety of rare and threatened species.

We hope and expect that the agency will carefully consider all meaningful alternatives and go beyond the admittedly "preliminary" information provided in the PSA. The agency should revisit these issues in detail and provide a full range alternatives as part of the Draft EIR for public review.

Thank you for the opportunity to submit these comments, and we look forward to participating in the project as the process moves forward. Please feel free to contact me for additional information at 535-654-5943 or at ianderson@biologicaldiversity.org

Best regards,

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Department of Interior

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APPLICATION FOR CERTIFICATION
FOR THE *IVANPAH SOLAR ELECTRIC*
GENERATING SYSTEM

DOCKET NO. 07-AFC-5
PROOF OF SERVICE
(Revised 7/2/09)

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DECLARATION OF SERVICE

I, Lisa T. Belenky, declare that on July 8, 2009, I served and filed copies of the attached, CBD Comments on PSA and DT plan dated July 8, 2009. The original document, filed with the Docket Unit, is accompanied by a copy of the most recent Proof of Service list, located on the web page for this project at: **[www.energy.ca.gov/sitingcases/ivanpah]**.

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I declare under penalty of perjury that the foregoing is true and correct.

Lisa T. Belenky

Avian Mortality at a Solar Energy Power Plant
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Source: *Journal of Field Ornithology*, Vol. 57, No. 2 (Spring, 1986), pp. 135-141
Published by: Blackwell Publishing on behalf of Association of Field Ornithologists
Stable URL: http://www.jstor.org/stable/4513113
Accessed: 14/12/2009 18:32

J. Field Ornithol., 57(2):135-141

AVIAN MORTALITY AT A SOLAR ENERGY POWER PLANT

By Michael D. McCrary, Robert L. McKernan,
Ralph W. Schreiber, William D. Wagner,
and Terry C. Sciarrotta

In 1979, the United States Department of Energy, in conjunction with the Southern California Edison Company (SCE) and the Los Angeles Department of Water and Power, initiated the construction of Solar One, the world's largest solar energy power plant (Fig. 1). Until the construction of Solar One, the use of the sun's energy to produce electrical power had not been attempted on this scale, and the environmental hazards of operation of a solar power plant were unknown. In this paper we report on bird mortality at Solar One.

STUDY AREA AND METHODS

Solar One is a 10 megawatt, central receiver solar power plant consisting of a 32-ha field of 1818, 6.9 × 6.9 m mirrors (heliostats) which concentrate sunlight on a centrally located, tower-mounted boiler, 86 m in height (Fig. 1). The reflective surface area of each heliostat is approximately 40 m^2, and the total for all heliostats is approximately 72,500 m^2. When not directed at the tower during morning startup, testing, and maintenance, some or all of the heliostats are focused on standby points, four small areas (approximate diameter = 5 m) of sky around the tower at a height of 80 m. Temperatures within the standby points vary with the number of heliostats focused on them and the reflectivity of an object placed within them, but the temperature can be high enough to burn feathers and small insects.

Solar One is located in the Mojave Desert, 4 km east of Daggett, San Bernardino County, California (34°52'N, 116°51'W). The dominant desert plant community in this area is creosote bush (*Larrea divaricata*) scrub, although abandoned and active agricultural fields (alfalfa) and extensive (53 ha) evaporation ponds (Fig. 1) are adjacent to Solar One.

We visited Solar One approximately once per week (2–3 days per visit) on 6 occasions from 3 May through 8 June 1982 and on 34 occasions from 16 September 1982 through May 1983. During each visit 1–2 observers searched the facility for any evidence of bird mortality. Although searches were not conducted in a fixed pattern, the entire facility was covered during each visit. Bird carcasses were readily found because of the sparse vegetation and level ground of Solar One. Experiments involving the placement of 19 bird carcasses of various species within and just outside (<200 m) the fenced facility were conducted in May and September 1982 to measure the rate of bird carcass removal by scavengers. These carcasses were checked periodically until removed by scavengers or decomposed.

FIGURE 1. Aerial view of Solar One: (A) heliostat field, (B) central receiver tower, (C) evaporation ponds. Tower height = 86 m, diameter of field = 765 m.

To determine the impact of bird mortality on local populations, 1–2 observers conducted surveys of relative avian abundance within an area of approximately 150 ha surrounding Solar One, concentrating on the facility grounds (32 ha), evaporation ponds, and agricultural fields. These surveys were conducted on at least 2 d per visit for 3–4 h/d.

RESULTS

Solar One related animal mortality.—During approximately 40 wks of study, we documented 70 bird fatalities involving 26 species at Solar One (Table 1). The mean rate of mortality between visits was 1.7 birds ± 1.8 SD (*n* = 40, range 0–7). Results of the scavenger bias experiments indicate that from 10–30% of carcasses were removed between searches, thus, the actual rate of mortality may have been from 1.9–2.2 birds. Two causes of avian mortality were identified at Solar One, colliding with structures and burning from standby points.

The most frequent form of avian mortality was from collisions with Solar One structures. We documented 57 (81%) bird deaths (20 species) from collisions (Table 1). In most cases the cause of death was determined by the presence of broken bones (usually mandibles or wings) found through external examination. From the location of birds in relation to structures, most (>75%) died from colliding with the mirrored heliostats, although a dead Blue-winged Teal (*Anas discors*) with a broken wing was found on a platform of the receiver tower. On one occasion

TABLE 1. Avian mortality from burning and collisions at Solar One, 1982–1983.

Burn fatalities		Collision fatalities	
Species	Number of individuals	Species	Number of individuals
Vaux's Swift (*Chaetura vauxi*)	1	Eared Grebe (*Podiceps nigricollis*)	11
White-throated Swift (*Aeronautes saxatalis*)	2	Blue-winged Teal (*Anas discors*)	1
Hummingbird sp.	3	American Kestrel (*Falco sparverius*)	1
Cliff Swallow (*Hirundo pyrrhonota*)	2	American Coot (*Fulica americana*)	2
Barn Swallow (*Hirundo rustica*)	1	Black-necked Stilt (*Himantopus mexicanus*)	2
Barn Swallow (*Hirundo rustica*)	1	Sandpiper sp.	1
Yellow-rumped Warbler (*Dendroica coronata*)	1	Red-necked Phalarope (*Phalaropus lobatus*)	1
Wilson's Warbler (*Wilsonia pusilla*)	1	Bonaparte's Gull (*Larus philadelphia*)	1
Sparrow sp.	1	Mourning Dove (*Zenaida macroura*)	6
		Hummingbird sp.	1
		Horned Lark (*Eremophila alpestris*)	3
		European Starling (*Sturnus vulgaris*)	4
		Yellow-rumped Warbler (*Dendroica coronata*)	1
		MacGillivray's Warbler (*Oporornis tolmiei*)	1
		Savannah Sparrow (*Passerculus sandwichensis*)	3
		White-crowned Sparrow (*Zonotrichia leucophrys*)	2
		Dark-eyed Junco (*Junco hyemalis*)	1
		Red-winged Blackbird (*Agelaius phoeniceus*)	3
		Western Meadowlark (*Sturnella neglecta*)	1
		Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	2
		Brewer's Blackbird (*Euphagas cyanocephalus*)	5
		House Finch (*Carpodacus mexicanus*)	4
Total	13	Total	57

in May 1982 a Solar One employee observed 4 Mourning Doves (*Zenaida macroura*) die in a collision with a single heliostat.

Thirteen (19%) birds (7 species) died from burning in the standby points (Table 1). Although we never observed a bird fly through one of the standby points, the heavily singed flight and contour feathers indicated that the birds burned to death (Fig. 2). Six (46%) of these fatalities involved aerial foragers (swifts and swallows) which are apparently more susceptible to this form of mortality because of their feeding behavior. Three of these aerial foragers died during a 2-wk period in May 1982, corresponding with the presence of the highest numbers of swifts and swallows observed (>500 per d), and an extensive period of heliostat testing when the occurrence and intensity of standby points was probably greater than at other times.

Relative avian abundance.—During 102 d from May–June 1982 (18 d) and September 1982–May 1983 (84 d), we recorded 107 bird species (daily mean = 16.7 ± 6.1 SD, n = 102) in the immediate area (150 ha) of Solar One. The mean daily count for individuals was 314 ± 203 SD (range 148–1040). Most avian species recorded at Solar One were migrants and only 15 species are year-round residents, with Horned Larks (*Eremophila alpestris*), European Starlings (*Sturnus vulgaris*), and House Finches (*Carpodacus mexicanus*) the most common breeding birds.

Of the habitats surveyed in this study, the evaporation ponds were the most heavily used by birds. Seventy percent of all species were recorded at least once at the ponds, and 45% were recorded only at the ponds; the majority of daily counts recorded mostly waterbirds.

DISCUSSION

Creosote bush scrub, which characterizes much of the undisturbed portions of the Mojave Desert near Solar One, is usually only sparsely inhabited by birds. The avian community of similar habitat in Arizona is usually less than 20 species (Tomoff, Ecology 55:396–403, 1974). However, we recorded 107 species in the vicinity of Solar One, 15 of which breed in the area. The special attraction of Solar One to birds is most likely related to the presence of a large, man-made water impoundment and irrigated agricultural fields, both of which produce an abundance of insects. Naturally occurring open water sources in the Mojave Desert are rare and usually ephemeral, while the man-made ponds near Solar One are permanent.

The most frequent form of avian mortality at Solar One during this study was from collisions with structures, primarily heliostats. Avian collisions are an inevitable by-product of almost all man-made structures (see Avery et al., FWS/OBS-80/54, 1980). Reflective surfaces are especially prone to collisions (Klem, Ph.D. thesis, Southern Illinois Univ., Carbondale, 1979), and it is not surprising that collisions with mirrored heliostats occur on a somewhat regular basis considering the reflective surface area of Solar One.

A form of avian mortality unique to solar central receiver power plants is burning in standby points. Death after being burned was infrequent in occurrence at Solar One, being in part a function of the frequent absence and variable intensity of standby points and the number of aerial foragers (swifts and swallows) in the airspace over Solar One.

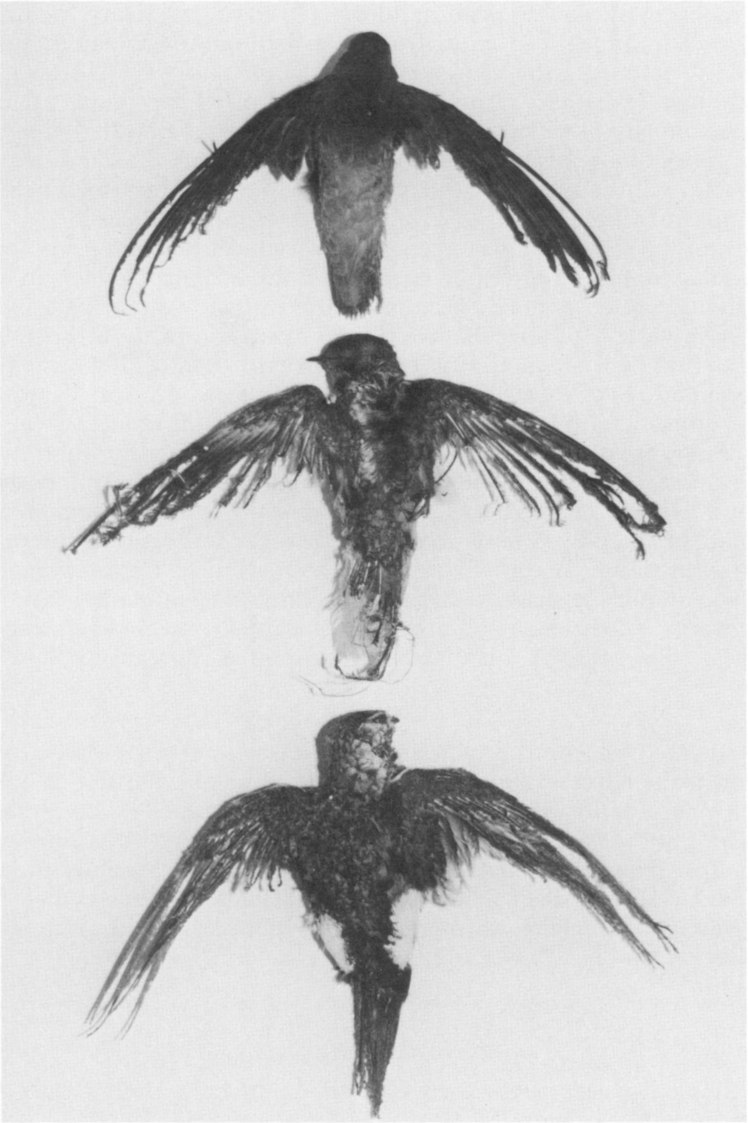

FIGURE 2. Three birds burned in standby points at Solar One. Top to bottom: Vaux's Swift (*Chaetura vauxi*), Barn Swallow (*Hirundo rustica*), and White-throated Swift (*Aeronautes saxatalis*). Note the heavily singed rectrices and remiges especially in the Barn Swallow.

Considering all known avian fatalities (70 birds) at Solar One during this study the impact of the facility on birds after construction appears minimal. Comparing the estimated rate of mortality (1.9–2.2 birds per wk) and mean relative avian abundance (314 birds per count) recorded in the vicinity of Solar One, only 0.6–0.7% of the local population present at any given time may have been affected during this study. The effect on the total population using the region in a year is obviously much less, but is unestimatable.

The results of this study suggest that, to reduce their impact on birds, future solar central receiver power plants in the Mojave Desert and other areas should not be sited in close proximity to open water or agricultural fields. The variety of species involved in avian mortality at Solar One indicates that caution should be taken when siting a solar power plant near populations of rare, threatened, or endangered species. If possible, the occurrence and intensity of standby points should be kept to a minimum. Since Solar One is only a 10 megawatt pilot facility, future projects designed to produce hundreds of megawatts will require several thousand heliostats and much taller receiver towers. The greater magnitude of these facilities may produce non-linear increases in the rate of avian mortality when compared to Solar One and extrapolations from this study should be made with caution. The removal of large tracts of desert from biological production for solar power generation and the ecological effects caused thereby should also be of concern.

SUMMARY

We studied avian mortality at an operating solar central receiver power plant in the Mojave Desert of southern California. During 40 wks of study we documented the deaths of 70 birds (26 species). The estimated mortality rate was 1.9–2.2 birds per week. Fifty-seven (81%) birds of 20 species died from collisions with Solar One structures, mainly the mirrored surfaces of heliostats. Thirteen (19%) birds (7 species) died from burns received by flying through standby points. The impact of this mortality on the local bird population is considered minimal (0.6–0.7% per wk).

ACKNOWLEDGMENTS

We thank J. Reeves (Research and Development, Southern California Edison Co.), P. Skvarna (SCE Site Manager of Solar One), D. Elliott (U.S. Department of Energy Project Director), and all other Solar One personnel for their valuable assistance on this project. P. Flanagan and G. Sawyer provided assistance in the field, and C. Barrows, P. Bloom, E. H. Burtt, Jr., J. Gore, and D. Klem provided editorial comments on the manuscript. This project was financially supported by a contract from the Southern California Edison Company to the Los Angeles County Museum of Natural History Foundation.

Los Angeles County Museum of Natural History, Section of Ornithology, 900 Exposition Blvd., Los Angeles, California 90007 (MDM, RLM, RWS, WDW); *Southern California Edison Company, Research and Development, P.O. Box 800, Rosemead, California 91770* (TCS). Received 1 Oct. 1985; accepted 24 Jan. 1986.

Fueling Population Growth in Las Vegas: How Large-scale Groundwater Withdrawal Could Burn Regional Biodiversity

JAMES E. DEACON, AUSTIN E. WILLIAMS, CINDY DEACON WILLIAMS, AND JACK E. WILLIAMS

Explosive growth in Las Vegas, Nevada, has stimulated demand for additional water supplies. To meet these needs, local officials hope to obtain rights to about 200,000 acre-feet (246.70 million cubic meters [m^3]) per year from a regional groundwater aquifer extending from Salt Lake City, Utah, to Death Valley, California. Officials from satellite communities are pursuing rights to an additional 870,487 acre-feet (1.07 billion m^3) per year. If granted, these new permits would trigger declines in groundwater across at least 78 basins covering nearly 130,000 square kilometers. Water-rights decisions have historically interpreted economic development as a more compelling public interest than maintenance of natural systems. If economic development continues to drive allocation decisions, consequent declines in the water table, spring discharge, wetland area, and streamflow will adversely affect 20 federally listed species, 137 other water-dependent endemic species, and thousands of rural domestic and agricultural water users in the region. Reducing consumption and implementing cost-effective technologies, such as recovery of urban runoff and shallow saline groundwater, indirect reuse of potable water, and desalinization, offer ways to meet metropolitan and ecological needs within the limits of the resource.

Keywords: groundwater, water rights, public trust, endangered species, ecological integrity

Some of the most rapid population growth in the United States is occurring in intermountain western and southwestern urban areas, where water is in short supply and aquatic ecosystems are stressed (Naiman and Turner 2000, Fitzhugh and Richter 2004). As a result, municipal water consumption is on the rise, and water from rural areas is being shifted toward municipal uses. Competition for water is felt keenly in southern Nevada, where water is scarce, human population growth is explosive, and conflicts over biodiversity and the human need for water have a long and litigious history.

With an annual growth rate of 5.5 percent and a population exceeding 1.8 million, Las Vegas, Nevada, is among the fastest-growing metropolitan areas in the nation. After use of local groundwater produced up to 2 meters (m) of land subsidence and a 91-m decline in the water table in parts of the metropolitan area (Burbey 1995), the community became dependent primarily on the now drought-stricken Colorado River as its major source of fresh water. Water demand has reached the limits of the current supply, exacerbated by daily per capita consumption that ranks among the nation's highest (both in terms of single-family consumption, at 660 liters [L] per person per day, and of total systemwide consumption, at 971 L per person per day; Western Resource Advocates 2006).

The Southern Nevada Water Authority (SNWA) is pursuing a multipronged approach to meet the growing municipal water demand (SNWA 2005). As a stopgap measure, in 2004 the SNWA purchased 1.25 million acre-feet (1.54 billion m^3) of Colorado River water from Arizona to be delivered over the next 15 years. The SNWA has advocated vigorously for new operating rules, currently under review by the secretary of the Department of the Interior, to be used during severe drought conditions on the Colorado River. The SNWA also plans to

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tap a regional deep carbonate aquifer extending across central and southern Nevada from Utah to California (SNWA 2004), a tactic simultaneously being pursued by other Nevada counties (e.g., Lincoln, Nye, and White Pine).

Great Basin spring systems, although small and isolated, harbor a large proportion of the region's biodiversity and have received significant conservation attention (Deacon and Minckley 1991, Sada and Vinyard 2002). Twenty species and subspecies listed under the federal Endangered Species Act (ESA) depend on springs, spring-fed wetlands, and streams in the 78-basin area most likely to be affected by the proposed SNWA groundwater withdrawals (table 1). Many listed taxa are "umbrella species" that provide protection to little-known, nonlisted sympatric species, including at least 137 spring-dependent animal taxa—primarily locally endemic aquatic springsnails, insects, and fishes. The Nevada Natural Heritage Program (2005) identifies 347 sensitive taxa within the area.

Our purpose here is to critically examine the SNWA proposals for large-scale groundwater withdrawal, evaluate their potential impacts on aquatic biodiversity, and evaluate whether Nevada water law can avoid decisions that are detrimental to the public interest. The literature demonstrates that deep carbonate and shallow basin-fill aquifers are interconnected across the various basins likely to be affected by groundwater withdrawal, and that the approval of the SNWA applications for water rights is likely to reduce or eliminate many spring and wetland communities in the region, with consequent adverse impacts on the rich diversity of spring- and wetland-dependent endemic species. We contend that large-scale groundwater withdrawal in Nevada, the most arid state in the United States, poses a major underappreciated threat to biodiversity.

The groundwater flow system

Carbonate rocks, deposited in a shallow sea during the Paleozoic, underlie a 259,000-square-kilometer (km^2) carbonate-rock province in the eastern two-thirds of the Great Basin (Fiero 1986). During the late Mesozoic, compression, uplift, and low-angle thrust faulting deformed this carbonate layer. East–west extension in the mid-Tertiary thinned the carbonate section, caused block faulting, and gave rise to the north–south orientation of mountain ranges characteristic of the basin and range. Later, predominantly northeast–southwest-oriented fractures and joints formed throughout the brittle limestone and dolomite deposits (Winograd and Thordarson 1975).

Although much of the original 12-km-thick carbonate layer in Nevada has become deformed, dismembered, and thinned, there remains a 110- to 160-km-wide central corridor of contiguous carbonate rocks, typified by an extensive interconnected subterranean fracture network extending 1 to 1.5 km or more below land surface. This corridor integrates a regional-scale drainage network extending from near the Utah–Nevada border through southern Nevada's Spring Mountains and into California, and is capable of transporting large volumes of water (Riggs et al. 1994).

Table 1. Native spring-dwelling and riparian species known from the area of projected groundwater decline in Lincoln, Clark, White Pine, Nye, and eastern Esmeralda counties, Nevada; eastern portions of Inyo and San Bernardino counties, California; western portions of Washington, Iron, Beaver, Millard, and Juab counties, Utah; and northwestern Mohave County, Arizona.

Taxon	Endangered species/ subspecies	Threatened species/ subspecies	Other species/ subspecies
Mammals	1	0	2
Birds	2	0	1
Fishes	11	2	31
Amphibians	0	0	4
Aquatic insects	0	1	50
Springsnails	0	0	49
Plants	1	2	NA
Total	15	5	137

NA, not available.

Note: Species and subspecies listed as endangered or threatened include the following: mammals, *Microtus californicus scirpensis;* birds, *Empidonax trailii extrimus* and *Rallus longirostris yumanensis;* fishes, *Plagopterus argentissimus, Gila seminuda, Rhinichthys osculus nevadensis, Moapa coriacea, Empetrichthys latos, Cyprinodon nevadensis mionectes, C. nevadensis pectoralis, Cyprinodon diabolis, Lepidomeda mollispinis pratensis, Lepidomeda albivallis, Crenichthys baileyi grandis, Cr. baileyi baileyi,* and *Crenichthys nevadae;* insects, *Ambrysus amargosus;* plants, *Centarium namophilum, Ivesia kingii* var. *eremica,* and *Nitrophila mohavensis.* A complete species listing is available from the authors.

Groundwater typically flows from high-elevation montane recharge areas to discharge areas in basin-fill sediments of valley lowlands. Flow occurs at various scales, resulting in the superimposition of numerous relatively shallow, localized basin-fill aquifers on the regionally integrated deep carbonate aquifer. Because of the fractured nature of the underlying carbonate rocks, water carried in the deep aquifer may originate from all elevations throughout the central corridor. Regardless, shallow aquifers discharge primarily by means of evapotranspiration and through local springs, whereas deep aquifers discharge mostly at regional warm springs (Prudic et al. 1995).

Regional springs in the 78 basins we examined are the primary natural discharge points from eight major groundwater flow systems (figure 1). Springs from Preston Big Spring southward to Ash Spring are supplied principally from montane recharge areas in east-central Nevada at the top of the regional drainage net. Muddy River springs are supplied principally from the north through the central corridor, but also may receive some recharge from nearby Sheep Mountains. Ash Meadows springs are supplied predominantly from recharge areas on the northern and northeastern slopes of the nearby Spring Mountains but, along with springs on the eastern side of Death Valley, are partially dependent on regional groundwater movement from the north-northeast through the central corridor (Dettinger et al. 1995). Las Vegas Valley and Pahrump Valley receive most of their groundwater from recharge in southern Nevada's Spring Mountains.

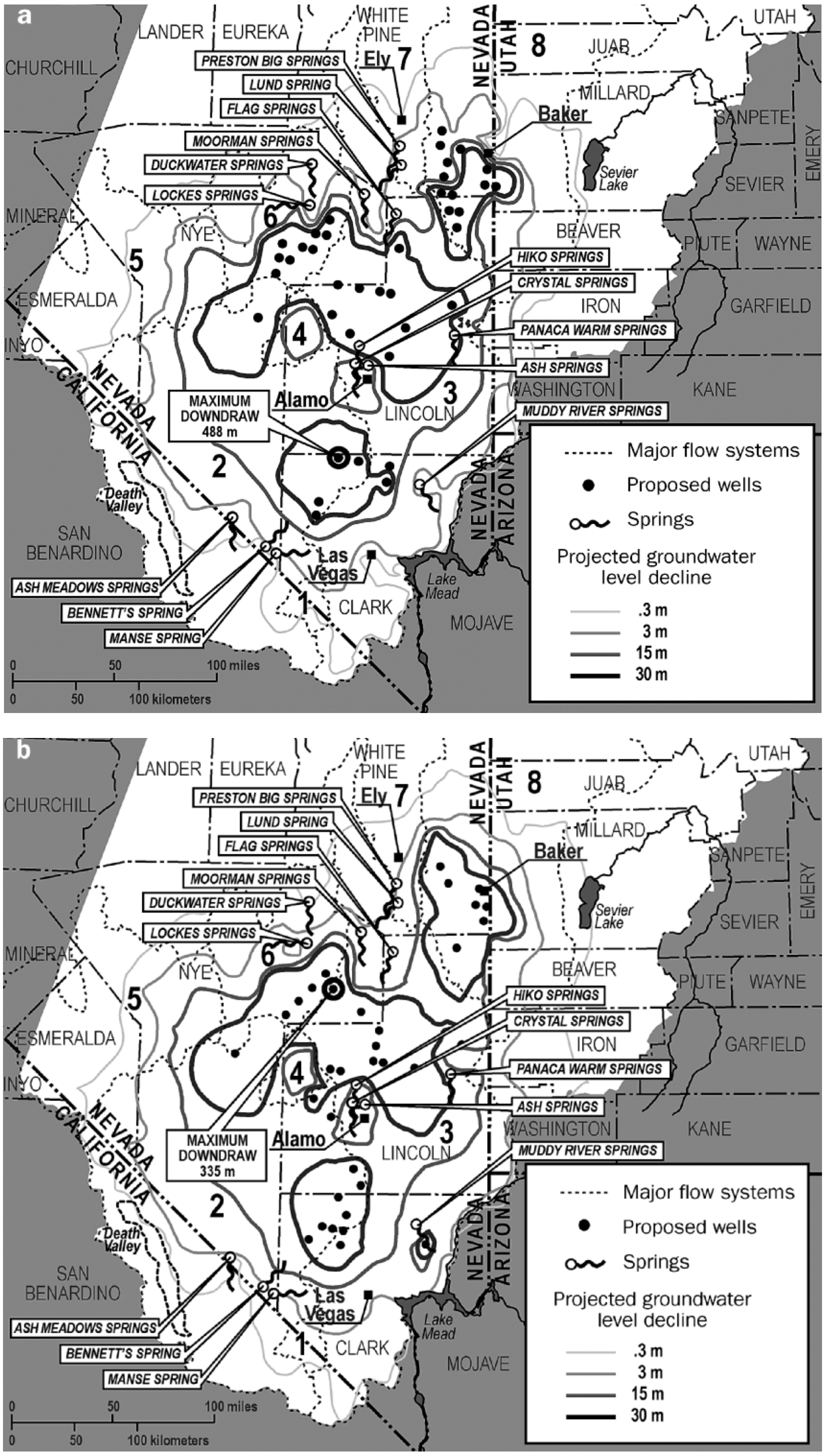


Figure 1. Simulated final steady-state groundwater level in (a) valley-fill and (b) deep carbonate aquifers in eight major flow systems of Nevada, Utah, and California, projected to occur as a consequence of pumping 180,800 acre-feet (223.01 million cubic meters) per year of water from specific well locations in specific quantities as proposed by the Southern Nevada Water Authority (SNWA). This simulation assumes no groundwater removal other than the 180,800 acre-feet (223.01 million cubic meters) per year projected to be pumped by the SNWA from 17 basins of east-central and southern Nevada. The eight major groundwater flow systems affected are numbered as follows: 1, Mesquite Valley; 2, Death Valley Flow System; 3, Colorado Flow System; 4, Penoyer Valley; 5, South-central Marshes Flow System; 6, Railroad Valley Flow System; 7, Goshute Valley Flow System; and 8, Great Salt Lake Desert Flow System. Modified from Schaefer and Harrill (1995) and Harrill and Prudic (1998).

The estimated annual groundwater recharge to the eight flow systems is about 900,000 acre-feet (1.11 billion m^3) per year (Harrill and Prudic 1998), with about 80 percent of that recharge attributable to the 78 basins we examined (table 2). Subsurface movement of water from one flow system to another supplements groundwater recharge from local sources. For example, approximately 21,000 acre-feet (25.90 million m^3) of water per year, principally from the White River flow system (a northern subdivision of the Colorado River flow system), supplements groundwater in the Death Valley flow system (Dettinger 1989). Because there is equilibrium between aquifer recharge and natural discharge, wells continuously extracting any part of the annual recharge virtually guarantee equivalent reductions in natural discharge (Dettinger et al. 1995).

Spring systems and groundwater withdrawal

The large number of endemic species occurring at regional springs in the carbonate-rock province is due in no small part to the reliability, consistency, and predictability of these wetland and aquatic habitats over millions of years. The springs in Ash Meadows, for example, have been major discharge points from the deep aquifer for the past two million to three million years, although three million years ago those springs were more widespread and discharge was greater than at present (Hay et al. 1986).

Climatic variation produced changes in groundwater levels in Ash Meadows over the past 116,000 years, including a 9-m decline in groundwater in the last 15,000 years as Pleistocene lakes disappeared (Szabo et al. 1994). Over the past century, the water table in the adjacent Pahrump and Las Vegas valleys has experienced an extreme drop attributable to groundwater pumping that dwarfs this climatically induced decline.

Development in Las Vegas Valley began in the early 1900s. Groundwater pumping led directly to the failure of major valley springs in about 1957 (Harrill 1976), causing extinction of the endemic Las Vegas dace (*Rhinichthys deaconi;* Miller 1984). Development in Pahrump Valley to the west of Las Vegas proceeded more slowly. Nonethe-

Table 2. Water rights currently allocated and applied for, expressed in acre-feet (and cubic meters) and as a percentage of perennial yield, in 78 basins likely to be affected by proposed large-scale groundwater pumping.

Flow system	Area in km^2	Basins with groundwater declines	Perennial yield in acre-feet (m^3)	Current rights in acre-feet (m^3)	Current rights, as percentage of perennial yield	Current rights plus rights applied for, in acre-feet (m^3)	Current rights plus rights applied for, as percentage of perennial yield
South-central Marshes	17,586	4	31,000 (38,237,937)	41,516 (51,209,232)	134	44,076 (54,366,946)	142
Death Valley	40,922	24	86,610 (106,831,862)	112,590 (138,877,720)	130	128,619 (158,649,200)	149
Railroad Valley	10,697	4	91,500 (112,863,588)	30,792 (37,981,373)	34	242,407 (299,004,632)	265
Penoyer Valley	1813	1	4000 (4,933,927)	14,461 (17,837,381)	362	17,662 (21,785,756)	442
Colorado	42,217	35	248,800 (306,890,281)	312,916 (385,976,203)	126	911,964 (1,124,891,030)	367
Goshute Valley	9428	1	70,000 (86,343,729)	95,928 (118,325,446)	137	119,349 (147,214,824)	170
Mesquite Valley	611	1	2200 (2,713,660)	1099 (1,355,597)	50	4407 (5,435,954)	200
Great Salt Lake Desert	46,620	8	185,500 (228,810,881)	125,700 (155,048,667)	68	480,489 (592,674,455)	259
Total	169,894	78	719,610 (887,625,865)	735,003 (906,612,851)	102	1,948,973 (2,404,022,800)	271

Note: Groundwater level decline is projected by Schaefer and Harrill (1995) only for parts of the South-central Marshes, Goshute Valley, and Great Salt Lake Desert flow systems, but is anticipated throughout all basins in the other five flow systems. Columns may not sum to totals because of rounding.

Source: Nevada Division of Water Resources Water Rights Database (20 February 2006; *http://water.nv.gov/Water%20Rights/permitdb/permitdb_index.cfm*); data for Snake and Hamlin valleys obtained from Utah Division of Water Rights, August 2005.

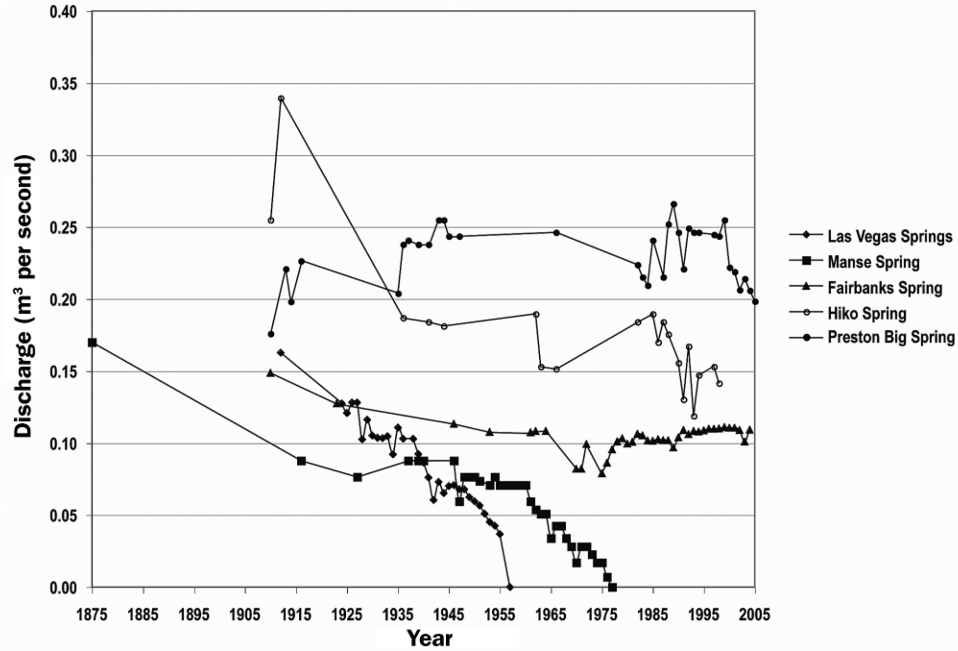


Figure 2. Annual mean discharge (cubic meters per second) from five representative springs in Nevada from 1875 to 2005. Data provided by Jon Wilson, US Geological Survey, Las Vegas, Nevada.

less, Raycraft Spring failed in 1957. Bennett's Spring dried in 1958, and Manse Spring followed in 1975 (Soltz and Naiman 1978, Harrill 1986), extirpating the endemic Pahrump poolfish (*Empetrichthys latos*) throughout its historic range (Deacon 1979) and eliminating a local population of the Spring Mountains pyrg (*Pyrgulopsis deaconi;* Hershler 1998). Groundwater declines of up to 30 m occurred by 1975 in Pahrump Valley (Harrill 1986), and declines of up to 91 m occurred by 1990 in Las Vegas Valley (Burbey 1995).

In Ash Meadows, after major groundwater development (initiated in the late 1960s) reduced both spring discharge and the water table (Dudley and Larson 1976), it was curtailed in 1977 and stopped by 1982 (Dettinger et al. 1995). Spring discharge recovered (e.g., Fairbanks Spring; figure 2), and the groundwater table rose steadily through 1987, but a slow decline began in 1988 and continues to the present (Riggs and Deacon 2004). An analysis by Bedinger and Harrill (2006) indicates that the decline is unrelated to climatic variation, and instead is due to groundwater withdrawal for irrigation at the Amargosa farms area about 25 to 30 km northeast of Devils Hole. Though some springs throughout the carbonate province tend to demonstrate stable flow, in many valleys there is evidence of decline (figure 2).

As of February 2006, existing groundwater permits authorized withdrawal of 735,003 acre-feet (906.61 million m^3) per year from the 78 basins we examined (table 2). This included 156,908 acre-feet (193.54 million m^3) per year for municipal uses in the urban areas of Las Vegas and Pahrump and about 578,095 acre-feet (713.07 million m^3) per year supporting the present agricultural and rural livelihoods of the area's residents.

These existing permits appropriate 102 percent of the 78-basin area's cumulative perennial yield, slightly more water than the state engineer has determined is available each year over the long term. However, permitted withdrawals are not spaced evenly across the landscape, but range from 0 to 1660 percent of the perennial yields estimated for individual basins. For example, valid groundwater rights now exist for 376 percent of perennial yield in Las Vegas Valley, 331 percent in Pahrump Valley, and 113 percent in the seven basins (combined in the state engineer's records) that include Ash Meadows. Existing rights exceed 100 percent of perennial yield in five of the eight major flow systems underlying the 78-basin area.

Looming threats

The Las Vegas Valley Water District (now the SNWA) filed 147 applications in 1989 for rights to unappropriated groundwater from 26 of the 78 basins overlying the region's major groundwater flow systems. Since they were originally submitted, some applications have been withdrawn and others modified to accommodate rural interests (SNWA 2004). At present, the SNWA hopes to obtain rights to 180,800 of the 330,000 acre-feet (223.01 million of the 407.05 million m^3) per year of groundwater for which they have applied. Wells to supply the water are to be drilled into shallow valley-fill aquifers as well as the deep carbonate aquifer of central, eastern, and southern Nevada. The first phase is planned to begin supplying water to Las Vegas as early as 2007, with additional wells and associated pipelines proposed over the coming 50 years (SNWA 2004).

The SNWA estimates that by 2050, it will need to add 375,000 to 475,000 acre-feet (462.56 million to 585.90 million m^3) per year to the 471,786 acre-feet (581.94 million m^3) per year now supplied predominantly from the Colorado River (SNWA 2005). Negotiations with other Colorado River basin states reached an agreement in principle on 3 February 2006 that the SNWA would not exercise its right to about 120,000 acre-feet (148.02 million m^3) per year of surface water from the Virgin and Muddy rivers so long as efforts by all basin states to augment flows of the Colorado River provide Nevada with the equivalent of 75,000 acre-feet (92.51 million m^3) per year (Jenkins 2006). The agreement also permits Nevada and other basin states to claim "augmentation credit" for water added to the river from other sources. If this augmentation credit is included in the final Colorado River drought condition operations rule, the SNWA can claim a credit for any Nevada groundwater that passes through the Las Vegas sewage system, including any water resulting from the new permits for which it has applied. This results in a 70 percent bonus and constitutes a substantial additional incentive to develop the proposed groundwater project.

Groundwater to be removed from regional aquifers by the SNWA does not represent the total anticipated new demand on those aquifers. Stimulated by Las Vegas's growth, satellite communities within a few hours' drive of Las Vegas (e.g., Coyote Springs, Mesquite, Pahrump, Sandy Valley, Prim, and Lincoln County communities) are being planned or are expanding rapidly. As of 20 February 2006, those satellite communities were responsible for most of the pending applications for an additional 870,500 acre-feet (1.07 billion m^3) per year of groundwater from the 78 basins.

Probable future effects of groundwater development

Following the 1989 applications by the Las Vegas Valley Water District for rights to all unappropriated groundwater in much of eastern, central, and southern Nevada, considerable effort was directed toward evaluating the probable impacts of removing a total of 180,800 acre-feet (223.01 million m^3) of groundwater annually from the locations, and in quantities desired by the SNWA. Schaefer and Harrill (1995) produced a conceptual model of the effects on the regional groundwater table, based on the assumption that the project now administered by the SNWA was the only source of groundwater removal throughout the region. Their work suggested that effects would be evident throughout the 78 basins examined here. Schaefer and Harrill's work was evaluated and compared with the SNWA's ongoing modeling efforts by Principia Mathematica (1997), which developed its own numerical model. Several groundwater models have been developed for specific basins within the area of probable impact (Durban 2006, Elliott et al. 2006, Myers 2006), most recently focusing on Spring Valley, from which the SNWA hopes to extract about half of the 180,800 acre-feet (223.01 million m^3) per year it seeks.

Except for the SNWA model, all research models produced results consistent with those of Schaefer and Harrill (1995), which projected groundwater level declines of about 0.3 to 488 m throughout 78 basins extending from Sevier Lake, Utah, to Death Valley, California. They suggested that a new steady state might be reached in 100 to 200 years, with groundwater level declines of 15 to 152 m predominating in both shallow and deep aquifers. Evapotranspiration throughout the region would decline as water tables dropped below the level of phreatophytic root penetration. Over the first 100 years, regional springs fed by the carbonate aquifer would lose about 2 to 14 percent of their flow. They would continue to decline over the next 100 years, and might not stabilize before failing. The divergence of these conclusions from those of the SNWA is due largely to the fact that SNWA modelers tended to estimate higher levels of precipitation-induced recharge and evapotranspiration-induced discharge than other modelers. This tendency is particularly evident when comparing the model submitted by the SNWA in support of the application for water rights in Spring Valley (Durban 2006) with the models submitted by the Western Environmental Law Center (Elliott et al. 2006, Myers 2006) in support of the center's protest against those applications.

Development dreams

While the location, depth, and quantity of withdrawal strongly influence the response in the aquifer, even the addition of only the incremental amount sought by the SNWA to the amount withdrawn under existing rights will produce greater evapotranspiration, spring discharge, and reductions in the groundwater table than those simulated by Schaefer and Harrill (1995). Within the 78 basins examined herein, total water demand would be increased to 127 percent of perennial yield by adding only the 180,800 acre-feet (223.01 million m^3) per year sought by the SNWA. Addition of the 870,487 acre-feet (1.07 billion m^3) per year sought by satellite communities would push demand to about 1.8 million acre-feet per year (2.2 billion m^3), or 250 percent of the region's estimated perennial yield. Approval of all applications pending as of February 2006 would put aquifer demand at 271 percent of perennial yield, although the state engineer, in accordance with decisions based on state law, is likely to authorize permits for less water than has been requested.

In Lincoln County, applications for groundwater rights by Vidler Water Company tend to locate points of withdrawal closer to regional discharge areas than do applications by the SNWA. Consequently, groundwater pumping by Vidler most likely will affect regional spring discharge more quickly than will SNWA's pumping, the impacts of which probably will manifest only decades later. Regional springs most likely to be influenced first by Vidler and later by SNWA wells include the Muddy River Springs and the large warm springs in Panaca Valley (Panaca Warm Springs), Pahranagat Valley (Ash, Crystal, and Hiko springs), and White River Valley (Preston Big, Lund, Moorman, and Flag springs).

In Nye County, proposed SNWA wells are likely to affect regional spring discharge in Railroad Valley (Duckwater, Lockes, and other springs) and Ash Meadows. Though the response will be long delayed by distance from the wellhead, regional springs in Ash Meadows are most likely to be adversely influenced by SNWA wells proposed for Indian Springs, Three Lakes, and Tikaboo valleys in the northeastern portion of the Ash Meadows flow system (Riggs and Deacon 2004). Even before a substantial reduction in spring discharge occurs in Ash Meadows, the first impact on existing water rights may be a lowering of the water level at Devils Hole, the one place in the entire carbonate-rock province where a surface-water right is objectively tied to groundwater level. In fact, there is mounting evidence to suggest that groundwater pumping from the regional aquifer already is producing a decline in the water level at Devils Hole (Bedinger and Harrill 2006).

State water management

The state engineer manages groundwater and surface waters under Nevada laws, which recognize connections between the two. Conflicts between users, whether of surface water or groundwater, are resolved according to prior appropriation principles. Thus, senior water rights, both surface and groundwater, limit junior water rights—a limitation that would constrain the groundwater withdrawal plans discussed above.

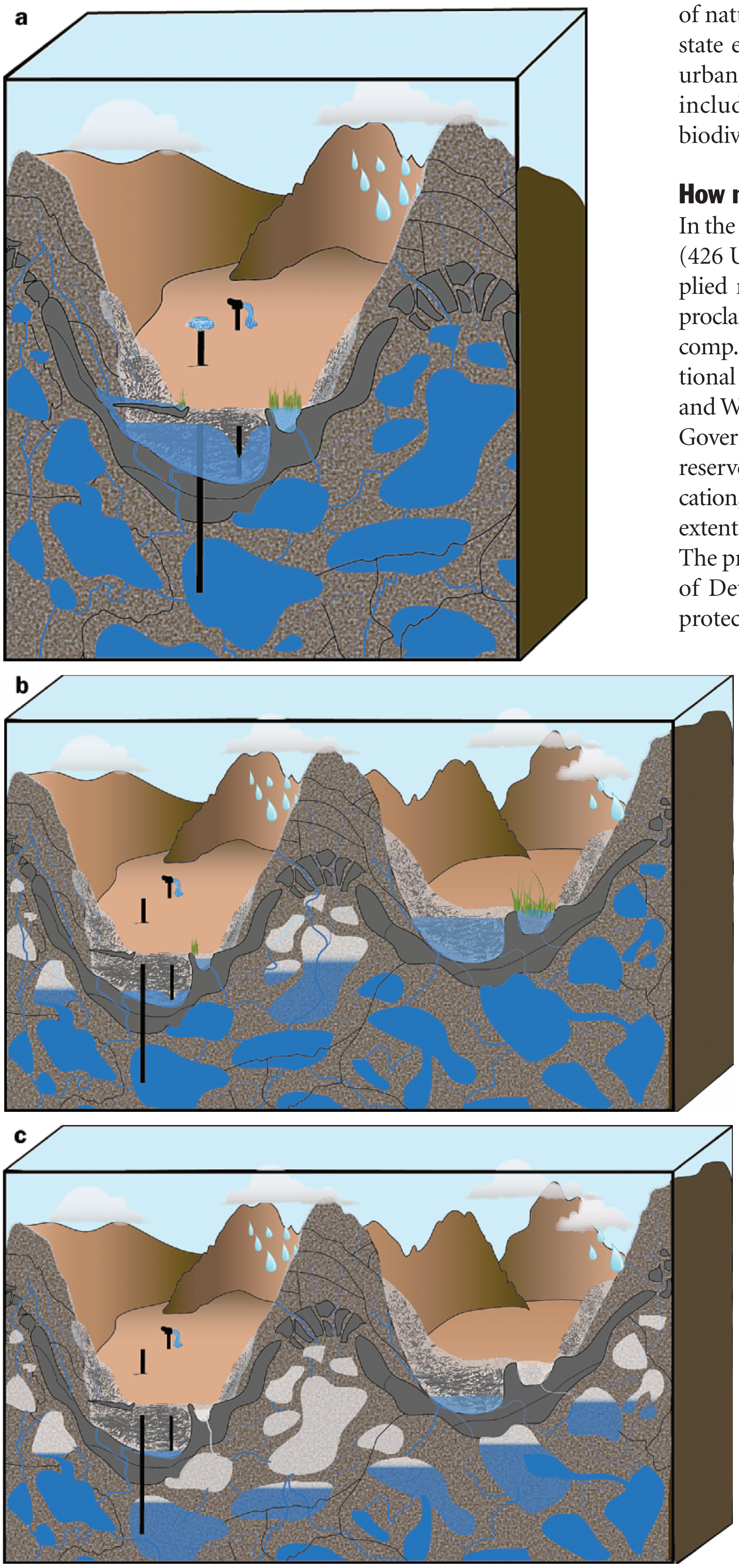
In evaluating the potential impacts of proposed groundwater permits on existing rights, the state engineer must make a determination of water availability based on the aquifer's perennial yield (similar to, but distinct from, sustainable yield). Permits beyond the perennial yield of the target aquifer may not be issued.

The Nevada Division of Water Resources' (1992) definition of perennial yield (i.e., "the amount of usable water from a ground-water aquifer that can be economically withdrawn and consumed each year for an indefinite period of time...[so long as it does] not exceed the natural recharge to that aquifer and ultimately is limited to maximum amount of discharge that can be utilized for beneficial use") can be a substantial barrier to conservation efforts. Although this definition conceptually prohibits the mining of groundwater, it offers little or no protection for surface water and thus is not a standard amenable to the maintenance of wetlands, springs, stream flows, or biodiversity. It also fails to maintain the groundwater table or subsurface interbasin flows. Furthermore, the technical accuracy of perennial yield estimates for some local and regional aquifers has been questioned (SNWA 2003).

Malmberg's (1967) estimate of perennial yield for Pahrump Valley provides an excellent example of the methods and assumptions commonly used. The maximum "salvageable discharge" available for appropriation included (a) all net spring discharge, (b) estimates of evapotranspiration from areas of shallow groundwater, (c) estimates of water salvageable from the amount that leaves the shallow aquifer as subsurface outflow from the basin, and (d) estimates of water salvageable from the amount that leaves the basin as subsurface outflow in the deep aquifer.

This method of determining perennial yield anticipates that permits issued will dry all springs and kill all phreatophytes, with attendant losses in biodiversity. It anticipates lowering of the groundwater table, a consequent increase in pumping costs, and the likelihood of land subsidence. It foresees reductions in both shallow and deep interbasin subsurface flows that supply down-gradient basins and their springs, thereby establishing a drain on shallow aquifers in surrounding valleys and in the regional deep carbonate aquifer (figure 3). These predictable consequences result directly from the issuance of permits equivalent to 100 percent of perennial yield. Unfortunately, despite the clear requirements of the law, permits commonly are issued for many times that amount.

Clearly, several factors confound attempts to unambiguously quantify the extent of expected detrimental impacts. Predicting the final steady state of the groundwater system in response to massive groundwater removal is complicated by disagreement over recharge from precipitation, discharge from evapotranspiration, connectivity among aquifer components, and the time required to reach a new equilibrium. There is no question, however, that the state's definition of, and methodology for determining, the quantity of water that legally may be withdrawn fails to envision the maintenance of natural systems. As a result, it is nearly impossible for the state engineer to issue groundwater permits in support of urban development while protecting existing water rights, including those concerning recreational resources and biodiversity.



How might protection be achieved?

In the 1976 US Supreme Court case *Cappaert v. United States* (426 U.S. 128), the court ruled that Devils Hole had an implied reservation of water, noting that a 1952 presidential proclamation (Proclamation no. 2961, 3 CFR 147 [1949–1953 comp.]) made Devils Hole a disjunct part of Death Valley National Monument (now Death Valley National Park; Deacon and Williams 1991). The court stated that "when the Federal Government withdraws its land from the public domain and reserves it for a federal purpose, the Government, by implication, reserves appurtenant water then unappropriated to the extent needed to accomplish the purpose of the reservation." The presidential proclamation specified that the withdrawal of Devils Hole from the public domain was intended to protect the "unusual features of scenic, scientific, and educa-

Figure 3. Conceptual diagrams of the effects of groundwater withdrawal on the variously integrated valley-fill and deep carbonate aquifers in Nevada. (a) Near-term effects: Wells in the valley-fill aquifer create a localized cone of depression; wells in the carbonate aquifer produce artesian flow; surface waters and biotic communities are imperceptibly affected. (b) Midterm effects: The water table in the valley-fill aquifer is substantially lowered, and local springs supported by this shallow aquifer fail; the carbonate aquifer loses its artesian pressure as the deep water table declines, and regional springs supported by this deep aquifer decline; groundwater from adjacent basins flows downgradient toward the reduced pressure caused by the lowering deep water table. (c) Late-term effects: A new steady state develops in both shallow and deep aquifers within the basin subjected to groundwater withdrawal; the downhill groundwater gradient toward the sites of withdrawal causes lowering of water tables and failure of local and regional springs in adjacent basins.

Legend

- ▨ Shallow, localized, valley fill aquifer
- ⬛ Impermeable layer, with fracture
- 🟦 Deep, regional, carbonate aquifer

tional interest...[including] a remarkable underground pool...[and] a peculiar race of desert fish." By this language, the federal government secured its right to the groundwater required to maintain the pool in Devils Hole and the endemic Devils Hole pupfish (*Cyprinodon diabolis*), vesting the right with a 1952 priority date. This implied reservation prohibits subsequent junior water users from receiving water rights that undermine conservation of the unique features of Devils Hole that led to its withdrawal, thereby benefiting not only the pupfish but also the endemic Devils Hole riffle beetle (*Stenelmis calida calida*), other species in the system, and the unique local ecology and geology.

The federal government also has reserved other centers of aquatic biodiversity because of their unique water resources and accompanying wildlife. Pahranagat National Wildlife Refuge (NWR), established in 1963 to provide habitat for migratory waterfowl, also protects an endemic subspecies of speckled dace (*Rhinichthys osculus* ssp.). Moapa NWR, established in 1979, provides habitat for the endangered Moapa dace (*Moapa coriacea*) and other rare aquatic spring endemics. Ash Meadows NWR, established in 1984 "to provide water habitat resources in Nevada for the protection of waterfowl and fish," protects a total of 15 federally listed species, including 9 that depend on springs or spring-fed wetlands, as well as 103 "at-risk" plant and animal taxa (USDOI 1982). If pressed, the courts would most likely determine that the federal government has implied rights to groundwater that are germane to the purposes of all these reservations, with a priority date corresponding to each reservation's date of withdrawal from the public domain. It is possible the implied reservation-of-water doctrine also would apply to lands acquired—as opposed to reserved—after statehood; however, that application has never been tested in court.

While the principles learned from *Cappaert* provide some protection when a species inhabits an area within reserved lands, the federal ESA may afford additional protection to threatened and endangered species that depend on habitat supported by discharge from groundwater aquifers. Current large-scale groundwater plans do not include the expenditure of federal monies, but the proposals do envision many well sites on and pipeline corridors across lands administered by the Bureau of Land Management, necessitating a federal permit and triggering the ESA's section 7 consultation provisions to ensure that federal actions do not jeopardize listed species. Furthermore, section 9 of the ESA prohibits "take" of listed species regardless of whether a federal action is involved.

All water within Nevada belongs to the public. The Nevada state engineer has a "continuing responsibility as a public trustee to allocate and supervise water rights so appropriations do not 'substantially impair the public interest in the lands and waters remaining'" (*Mineral County v. State Dep't of Conservation and Natural Res.,* 20 P.3d 800, 808–809 [2001], quoting *Illinois Central R.R. v. Illinois,* 146 U.S. 387, 452 [1892]). Traditionally, the public trust doctrine protected the public's interest in navigation, fishing, and commerce. However, the doctrine has evolved to encompass additional public values, including recreational and ecological uses.

Fahmy (2005) observed that, since the *Cappaert* decision, the state engineer increasingly has interpreted the "public interest" to include environmental values, such as endangered species. Beyond helping conserve "at-risk" species, Fahmy suggests that continuing judicious use of the public interest standard also could help maintain state sovereignty over water resources allocation and administration.

Achieving ecologically sustainable water use

Providing for the water needs of a growing Las Vegas Valley by relying on historical practices is a recipe for an ecological disaster involving loss of wetlands, spring-dependent species, and phreatophytic communities. New technologies can help increase water availability and efficiency of use, but in the long run they are futile unless combined with reduced growth of human populations. Reducing per capita consumption, however, could align Las Vegas residents' water use with the levels already realized in other major southwestern US cities (e.g., Albuquerque and Tucson; figure 4).

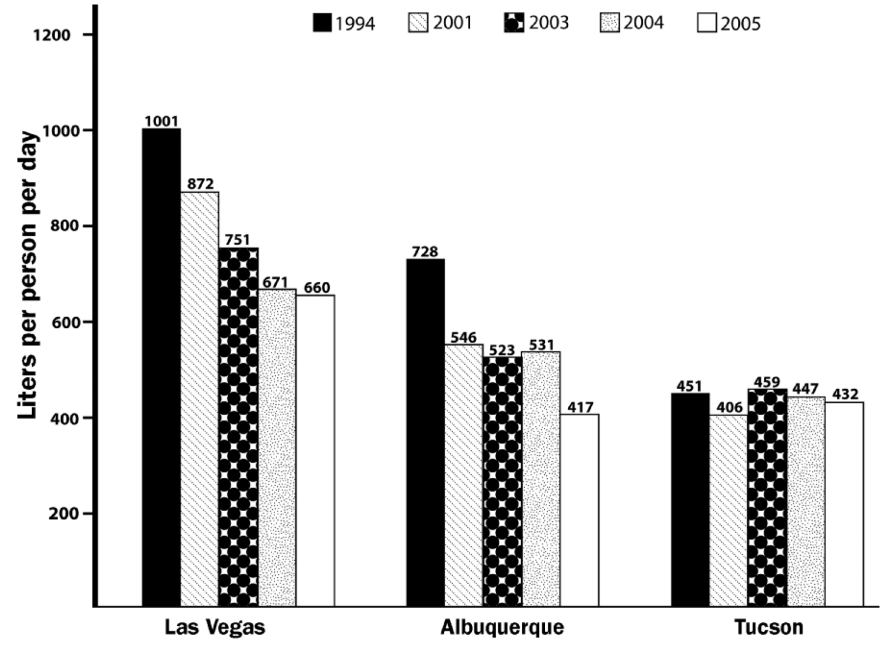


Figure 4. Changes in single-family, residential per capita water consumption in selected southwestern US cities from 1994 to 2005. Data from Western Resource Advocates (2006).

Water for lawns and other external uses outside the home offers the largest opportunity for cutting back single-family residential consumption. Mayer and colleagues (1999) calculated that approximately three-fourths of the residential water consumed in Las Vegas could be attributed to external rather than internal use. Western Resource Advocates (2006) calculated that, by 2030, converting 50 percent of the Las Vegas Valley's single-family residential landscaping to xeriscape would reduce demand by 80,000 acre-feet (98,678,547 m^3) per year, while indoor water conservation could reduce demand by more than 70,000 acre-feet (86,343,729 m^3) per year.

As in other southwestern cities, substantially lower consumption rates would result from increasing the price differential between tiers in the tiered rate structure already in place, and by implementing a range of other widely recognized measures to improve the efficiency of water use (Western Resource Advocates 2003, 2006). For new developments where retrofitting is unnecessary, low per capita consumption can be achieved even more easily simply by requiring serious water efficiency as a condition of development. Opportunities to reduce per capita water consumption to the low rate of 380 L per person per day have been identified for a new 648-hectare development in Las Vegas (Rocky Mountain Institute 2003). Comparable opportunities are available throughout the Las Vegas Valley.

As a reuse or recycling strategy for Las Vegas's tertiary effluent, membrane treatment could recover an amount of water comparable to that presently being obtained through "return-flow credit," a water-accounting system allowing Las Vegas to reuse water of Colorado River origin that is pumped from and then returned to Lake Mead. In addition, a membrane treatment system would make it possible to use saline water (originating as landscape irrigation water) from above the valley-fill aquifer. This shallow saline groundwater reportedly is accumulating at about 100,000 acre-feet (123,348,184 m^3) per year (SNWA 2006) and increasingly is flooding basements and creating other problems. Combined with urban runoff (which equals approximately 35,000 acre-feet [43,171,864 m^3] per year) and intermittently available floodwaters, both of which currently move through flood control channels to Las Vegas Wash and into Lake Mead, these sources have an apparent cumulative recovery potential of more than 135,000 acre-feet (166,520,048 m^3) per year. Following membrane treatment, this water could be used directly in the potable supply or indirectly as groundwater recharge. Membrane treatment would have the additional advantage of removing approximately 700,000 metric tons of salt per year (an amount approximating the total removed by all Bureau of Reclamation Colorado River Basin salinity control projects implemented to date), as well as a number of other environmental contaminants presently identified as problematic—including endocrine-disrupting compounds, personal care and pharmaceutical products, pesticides, chemicals used in plastic manufacturing, and artificial fragrances (Hinck et al. 2006)—and could substantially improve water quality in the Las Vegas Valley and the lower Colorado River.

One approach taken by several communities to manage consumption more efficiently is the direct or indirect reuse of highly treated effluent, a method that is becoming increasingly attractive as costs increase for water development, importation, and disposal. Reuse projects based on membrane treatment (microfiltration or reverse osmosis) of tertiary effluent are in place or under construction in Los Angeles, El Paso, Scottsdale, and many other places around the world (Durham et al. 2003). Such projects produce water that could be reused immediately in potable or irrigation supplies (direct reuse), reused later after recharging groundwater aquifers that are tapped to support domestic water supplies (indirect reuse), or both. Currently, most direct reuse projects are designed to meet irrigation water demands, whereas reuse projects designed to supply potable water generally involve indirect reuse. Preliminary calculations demonstrate that a membrane treatment system for Las Vegas would cost no more than a proposed effluent dilution project (about $800 million), would recover as much water as is recoverable by "return flow credit," and would improve water quality in Las Vegas and in the Colorado River downstream from Lake Mead (Walter Johnson, Clark County Water Reclamation District [retired], Las Vegas, Nevada personal communication, 17 November 2005).

Although the hydrogeology in southern Nevada is unique, concerns regarding the ecological impacts of groundwater withdrawal exist across the western United States. For example, the dependence of San Antonio, Texas, on groundwater from the Edwards Aquifer for municipal water supplies has had a growing impact on the endangered fountain darter (*Etheostoma fonticola*). Ultimately, minimum spring flows needed to avoid jeopardizing the darter's existence were established, and the Texas legislature mandated that the Edwards Aquifer Authority improve water management and conservation, leading San Antonio residents to reduce per capita water use by 24 percent between 1984 and 2000 (Fitzhugh and Richter 2004).

Richter and colleagues (2003) suggested defining ecologically sustainable water management as "protecting the ecological integrity of affected ecosystems while meeting intergenerational human needs for water and sustaining the full array of other products and services provided by natural freshwater ecosystems." Whether adhering to that standard of sustainability or to Nevada's considerably riskier standard of "perennial yield," we must acknowledge limits to water availability as we strive to strike a balance between human water demand and the needs of natural systems and future generations. Adherence to traditional standards virtually guarantees immediate ecological crises and unnecessary adversity for future generations. Those crises will manifest in litigation, "water wars," federal–state conflicts, and loss of springs, wetlands, phreatophytic communities, and biodiversity. Only through changed personal and community relationships with the Earth and its waters are we likely to succeed in conserving our ecological heritage while building a sustainable society.

Acknowledgments

Nelli Williams and Dave Melton applied their creative talents to the production of figures. Critical data, databases, and assistance were provided by Cristi Baldino, Glenn Clemmer, Terry Fisk, Shawn Goodchild, Walter Johnson, Zane Marshall, Tom Mayer, Eric Miskow, Rob Mrowka, Bernie Schlotthauer, Gary Scoppettone, Jon Sjoberg, Rose Strickland, Kurt Suchsland, Doug Threloff, and Jon Wilson. We are grateful to Adel Amos, Maxine Deacon, Alan Riggs, and anonymous reviewers for manuscript critiques. We sincerely thank these colleagues for their constructive, unselfish contributions.

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doi:10.1641/B570809
Include this information when citing this material.

SHORTER CONTRIBUTIONS

Copeia, 1998(3), pp. 702–705

Long-Term Sperm Storage in the Desert Tortoise (*Gopherus agassizii*)

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Many reptilian species exhibit the ability to store sperm in the female reproductive tract for extended periods of time (Gist and Jones, 1987; Birkhead and Moller, 1993). Sperm storage may be used to separate reproductive events such as copulation, fertilization, and hatching to optimize timing of these events (Birkhead and Moller, 1993). The redsided garter snake (*Thamnophis sirtalis*) ovulates and produces offspring in the spring but mate in the fall (Whittier and Crews, 1986). In this species, sperm from fall matings are thought to overwinter in the oviduct and fertilize ovum the following spring (Crews, 1984; Whittier and Crews, 1986). Reports of delayed egg laying in other species support the hypothesis that stored sperm are viable and used to fertilize subsequent clutches. Sperm storage has been inferred from oviductal flushings and/or observations of sperm in histological preparations of the oviduct (Gist and Jones, 1989; Gist et al., 1990). However, only controlled-mating experiments can demonstrate whether stored sperm are viable.

Sperm storage and multiple insemination may play a significant role in turtle reproduction (Gist and Jones, 1989). The ability to store sperm from previous matings and produce viable offspring using these sperm would be necessary for species whose male and female reproductive cycles do not coincide. Discordant cycles have been observed in temperate-zone turtles where time of mating and gamete maturation do not always occur simultaneously (Moll, 1979; Licht et al., 1985). In males of *Gopherus agassizii*, spermatogenesis begins in early summer and terminates with the onset of fall mating activity; females alternatively complete ovarian growth and lay eggs upon emergence from hibernation the following spring when male testes are fully regressed (Rostal et al., 1994).

In 1991, a large study was initiated at the Desert Tortoise Conservation Center to fill existing gaps in both basic and applied biology of the desert tortoise, *G. agassizii* (Spotila et al., 1994). A part of this large study was designed to delineate the reproductive cycle of male and female desert tortoises (Rostal et al., 1994). Reproductive groups consisting of three females and two males were maintained and monitored in seminatural enclosures from 1991–1993. Allozyme data were used to infer paternity and identify cases where stored sperm was used to fertilize eggs. Hatching success was recorded, and comparisons were made between clutches fertilized with sperm maintained in female reproductive tracts in excess of two years and clutches fertilized with sperm resulting from matings with males currently maintained in the enclosures.

MATERIALS AND METHODS

Fifty adult desert tortoises were placed in 10 seminatural enclosures at the Desert Tortoise Conservation Center (DTCC) in Las Vegas, Nevada. Tortoises at the DTCC were relocated from construction sites on the edges of Las Vegas in 1990 and 1991, as part of a research and conservation effort resulting from the recent listing of *G. agassizii* as a threatened species under the Endangered Species Act. Individuals were collected during late spring or early summer and weighed, measured, sexed, and tagged. Each reproductive group was comprised of three females and two males in individual 15 × 30 m field enclosures. Each enclosure contained five artificial burrows, natural vegetation, and two watering stations. Each enclosure was supplemented with alfalfa hay (Rostal et al., 1994). Animals were allowed to continue "normal" behavior (i.e., male-male combat and mating) and were kept in the enclosures for two complete breeding seasons (August 1991 to July 1993). Heparinized blood samples (3–5 mL) were collected via jugular venipuncture (Jacobson et al., 1992) and stored frozen for future analysis.

Females were observed closely, and ovaries and oviducts were scanned every two weeks during the nesting seasons by using an Aloka 500 V ultrasound scanner (Corometrics Medical Systems, Inc., Wallingford, CT 06492) to confirm

TABLE 1. POLYALLELIC ENZYME SYSTEMS DETECTED AND ELECTROPHORETIC CONDITIONS USED FOR THE DESERT TORTOISE, *Gopherus agassizii.*

Enzyme	Locus	Electrophoretic conditions[a]
Lactate dehydrogenase	Ldh-B	B
α-Naphthyl propionate	α-NP-Est	A
Malate dehydrogenase	mMdh-A	B
Glucose-6-phosphate isomerase	Gpi-A	B
Phosphogluconate dehydrogenase	Pgdh-A	B

[a] A: Lithium hydroxide pH 8.1 (Selander et al., 1971); B: Triscitrate pH 7.1 (Ayala et al., 1972).

when ovulation and subsequent egg deposition occurred (Rostal et al., 1994). Twelve clutches were collected during the second breeding season and incubated in individually sealed 850 mL tupperware containers. This allowed hatchling identification in specific clutches. Sixty-one hatchling tortoises were produced from these clutches, marked for identification, and transported to Georgia Southern University in 1993. Blood samples (0.5–1.0 mL) were taken from the identified offspring via jugular venipuncture in 1995 (tortoises were two years old).

Blood samples were thawed and proteins extracted from 0.5–1.0 mL whole blood by using 50 μl of grinding solution (0.01 M Tris, 0.001 M EDTA, 0.05 mM NaDP, pH = 6.8). Horizontal, starch-gel electrophoresis, using 12% starch gels composed of hydrolysed potato starch (Starchart Corp. lot W571-2), was conducted at 5 C. Electrophoretic conditions employed in this study are listed in Table 1. Allelic designations reflect relative differences in anodal electrophoretic mobility with the reference allele (= 100) being the most common allele found at a given locus (Rainboth et al., 1989). Other alleles were named relative to this standard and the origin (= 0).

To identify sperm storage, a comparison was made between genotypes within a clutch and genotypes of the mother and two males that occupied the same enclosure. Cases in which genotypes of offspring were not compatible with possible outcomes of matings between the female and two males were considered examples of sperm storage.

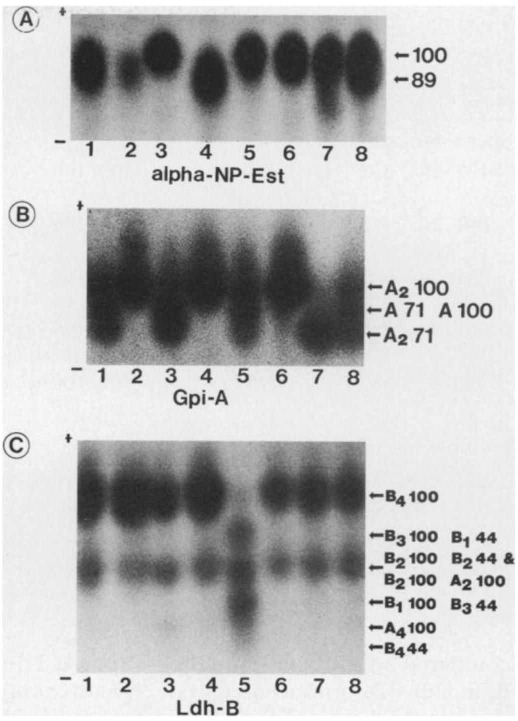

Fig. 1. Zymogram showing electrophoretic patterns of expression of gene products of the three enzyme systems used in this study. (A) Alpha-Napthyl propianate esterase; the individual in lane 4 is homozygous 89/89; specimens 3, 5, 6, and 7 are homozygous 100/100; and specimens 1, 2, and 8 are heterozygous 100/89. (B) Glucose-6-phosphate isomerase; lane 2, 4, and 6 individuals are homozygous 100/100; specimens 1, 3, 5, and 8 are heterozygous 100/71; and specimen 7 is homozygous 71/71. (C) Lactate dehydrogenase-A (designated with letter A before mobility number) and B (designated with letter B); specimen in lane 5 is heterozygous 100/44 at Ldh-B. All other specimens are homozygous for both the Ldh-A and Ldh-B loci.

RESULTS AND DISCUSSION

Allele products of five polyallelic loci were scored; three of these were used in detection of long-term sperm storage. The latter were alpha-naphthyl propionate esterase (α-Np-Est), lactate dehydrogenase (Ldh-B), and glucose-6-phosphate isomerase (Gpi-A; Fig. 1). Products of the remaining loci were monoallelic or did not resolve well: adenosine deaminase (Ada-2), hemoglobin (Hb), lactate dehydrogenase (Ldh-A), malate dehydrogenase (sMdh-A), NADP-dependent malate dehydrogenase (sMdhp-A), purine nucleoside phosphorylase (Pnp-1), peptidase (Pep-A, Pep-B, Pep-D, Pep-S), phosphoglucomutase (Pgm-A, Pgm-B), pyruvate kinase (Pk-A), and superoxide dismutase (sSod-A). Offspring from five of 12 clutches produced in 1993 appeared to be the result of fertilization with sperm stored from matings prior to the study in 1991 (Table 2). Tentative evidence for multiple paternity was found in one additional clutch in which genotypes at multiple loci were

Table 2. Genotypes of Embryos that Show Long-Term Sperm Storage and/or Multiple Insemination (Multiple Loci Analysis)

Mating Group F, M1, M2	Locus	Genotype of female	Genotype of male 1	Genotype of male 2	Genotypes of offspring
Sperm Storage					
195, 264, 432	Ldh-B	100/100	100/100	100/100	100/100 (4) 44/100 (2)
081, 264, 432	Ldh-b	100/100	100/100	100/100	100/100 (4) 44/100 (1)
304, 292, 995	Ldh-B	100/100	100/100	44/44	100/100 (3) 44/100 (2)
901, 200, 282	α-NP-Est	100/100	100/100	100/100	100/89 (5)
336, 498, 382	α-NP-Est	100/100	100/100	100/100	100/100 (1) 100/89 (4)
Multiple Insemination*					
874, 498, 382	Ldh-B	100/100	100/100	44/100	100/100 (8)
874, 498, 382	Gpi-A	71/71	100/100	100/71	100/71 (5) 71/71 (3)

*Taking both loci into account a mating between female 874 and male 498 is most likely at the Ldh-B locus, whereas a mating between female 874 and male 382 is most likely for Gpi-A locus.

compared within single-family groups. At Ldh-B, female 874 produced eight of eight offspring that would be predicted from a mating with male 498. However, at Gpi-A, three of eight offspring produced were consistent with a mating between female 874 and male 382, whereas five of eight offspring produced were consistent with a mating with male 498. Looking singly at either locus, offspring genotypes are concordant with matings of one or the other male. If both loci are taken into account, it is impossible to assign paternity solely to either male. In this case, the possibility of sperm storage cannot be excluded, because a definitive third allele is not present in the offspring.

No reduction in fertility was observed in clutches resulting from sperm stored in the females reproductive tract prior to introduction into the reproductive study enclosures. Mean hatching success (± SE) for all clutches was 95.8% (± 2.34, n = 12), whereas hatching success for clutches fertilized by sperm stored greater than two years was 97.1% (± 3.19, n = 5). These data are consistent with observations of viable hatchlings produced by females isolated from males for two years in other enclosures at the DTCC (Rostal, unpubl. data). Studies of other species, however, have reported a decrease in fertility as time increased from the previous mating (Goin et al., 1978; Davenport, 1995). In one case involving a caiman (Davenport, 1995), the animal was brought from Suriname and kept in a zoological setting where a single clutch was collected 488 days after the last contact with a male. Environmental and physiological stress factors may have played a significant role in the reduction of fertility observed. In the diamondback terrapin, *Malaclemys terrapin*, a sharp decline in fertility (87.9% to 30% hatching) was noted after the second year following isolation of females from males (Goin et al., 1978). This reduction in fertility was thought to result from sperm depletion rather than degradation of sperm in the oviduct (Gist and Jones, 1987). Further research is needed on sperm viability in other species.

Data from this study demonstrate sperm storage in *G. agassizii* and are consistent with reports that turtle species can store sperm for extended periods of time (Gist and Jones, 1987, 1989). Sperm-storage tubules located within the albumen-secreting gland region of the oviduct have been observed in several turtle species and are thought to provide a suitable environment for the storage of viable sperm (Gist and Fischer, 1993). Sperm storage thus appears to be a normal reproductive process that explains observations of delayed fertilization and a means for successful matings that are asynchronous with ovulation.

As with other temperate species of turtle, reproductive cycles of male and female *G. agassizii* are not synchronized (Rostal et al., 1994). Gamete maturation in females concludes in early spring when ovarian follicles reach ovulatory size. During this time, male testes are fully regressed, with mature sperm produced prior to hibernation three to four months earlier. Fall mating behavior suggests that sperm are inseminated into the female and then stored in sperm-storage tubules until emergence from hibernation in the spring. Gist et al. (1990) reported finding sperm in oviducts of *Chrysemys picta* and *Trachemys scripta* during the fall when copulatory behavior was observed. In addition, sperm could only be recovered from males during the fall when testes were fully mature (Gist et al., 1990), providing additional evidence supporting the sperm-storage hypothesis.

Gist et al. (1990) suggested that male/female interactions during spring mating may be essential for proper growth and maturation of reproductive organs and gametes in females. In *G. agassizi*, mating activity is observed in both the fall and spring. Presence of shelled eggs in oviducts following spring emergence and before mating activities, however, supports the notion of a functional, fall-mating period (Rostal et al., 1994). Seasonal changes in environmental conditions may precipitate asynchronous mating systems and the evolution of sperm storage in temperate turtle species.

ACKNOWLEDGMENTS

We thank M. Berkowitz and S. Slone (Bureau of Land Management) and K. Hicks (Savannah River Ecology Laboratory) for logistical assistance. Support for the research was provided through grant number GBFO-030191DRX from the Nature Conservancy, contract number DE-AC09-76SR00-819 between the U.S. Department of Energy and the University of Georgia's Savannah River Ecology Laboratory, Georgia Southern University Office of Research, and personal funds. Research was conducted under permits from U.S. Fish and Wildlife Service and the Nevada Division of Wildlife. Research was approved by the Georgia Southern University Animal Care Committee.

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Chelonian Conservation and Biology, 2007, 6(2): 229–251

A Genetic Assessment of the Recovery Units for the Mojave Population of the Desert Tortoise, *Gopherus agassizii*

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ABSTRACT. – In the 1994 Recovery Plan for the Mojave population of the desert tortoise, *Gopherus agassizii*, the US Fish and Wildlife Service established 6 recovery units by using the best available data on habitat use, behavior, morphology, and genetics. To further assess the validity of the recovery units, we analyzed genetic data by using mitochondrial deoxyribonucleic acid (mtDNA) sequences and nuclear DNA microsatellites. In total, 125 desert tortoises were sampled for mtDNA and 628 for microsatellites from 31 study sites, representing all recovery units and desert regions throughout the Mojave Desert in California and Utah, and the Colorado Desert of California. The mtDNA revealed a great divergence between the Mojave populations west of the Colorado River and those occurring east of the river in the Sonoran Desert of Arizona. Some divergence also occurred between northern and southern populations within the Mojave population. The microsatellites indicated a low frequency of private alleles and a significant correlation between genetic and geographic distance among 31 sample sites, which was consistent with an isolation-by-distance population structure. Regional genetic differentiation was complementary to the recovery units in the Recovery Plan. Most allelic frequencies in the recovery units differed. An assignment test correctly placed most individuals to their recovery unit of origin. Of the 6 recovery units, the Northeastern and the Upper Virgin River units showed the greatest differentiation; these units may have been relatively more isolated than other areas and should be managed accordingly. The Western Mojave Recovery Unit, by using the new genetic data, was redefined along regional boundaries into the Western Mojave, Central Mojave, and Southern Mojave recovery units. Large-scale translocations of tortoises and habitat disturbance throughout the 20th century may have contributed to the observed patterns of regional similarity.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; conservation genetics; distinctive population segment; evolutionary significant unit; management units; microsatellites; mitochondrial DNA; Mojave Desert; USA

The desert tortoise (*Gopherus agassizii*) is a widespread species (or possible species complex) occurring in the southwestern United States and northwestern Mexico (Fritts and Jennings 1994; Berry et al. 2002; Stebbins 2003). The US Fish and Wildlife Service (USFWS) federally listed the species as threatened under the Endangered Species Act, as amended, in the northern one third of its geographic range, specifically, populations living north and west of the Colorado River in the Mojave and Colorado deserts (USFWS 1990; Fig. 1). The listing occurred primarily because of population declines and habitat loss and deterioration, which were attributed to human activities. In recognition of the distinctiveness of the threatened populations, the USFWS developed the *Desert Tortoise (Mojave Population) Recovery Plan* (referred to herein as *Recovery Plan*) (USFWS 1994) and designated 26,087 km^2 of critical habitat (Berry 1997). About 83% of the critical habitat is on land managed by government agencies.

The federal listing of the desert tortoise as a threatened species brought about a redirection of government efforts to recover the species within its 4 southwestern states (California, Arizona, Nevada, and Utah). Several government agencies prepared new long-term management plans or amended older land-use plans to support recovery efforts (Berry 1997), a process that required more than 16 years. The extent of landscape affected by these efforts was significant and included parts of the Mojave Desert and the Colorado Desert (also called western Sonoran Desert). For convenience, the USFWS termed the populations within critical habitat as the "Mojave" population, when in fact they occur in both the Mojave and Colorado deserts. Herein, we follow this terminology. For populations in the Sonoran Desert of Arizona, we use "Sonoran" populations.

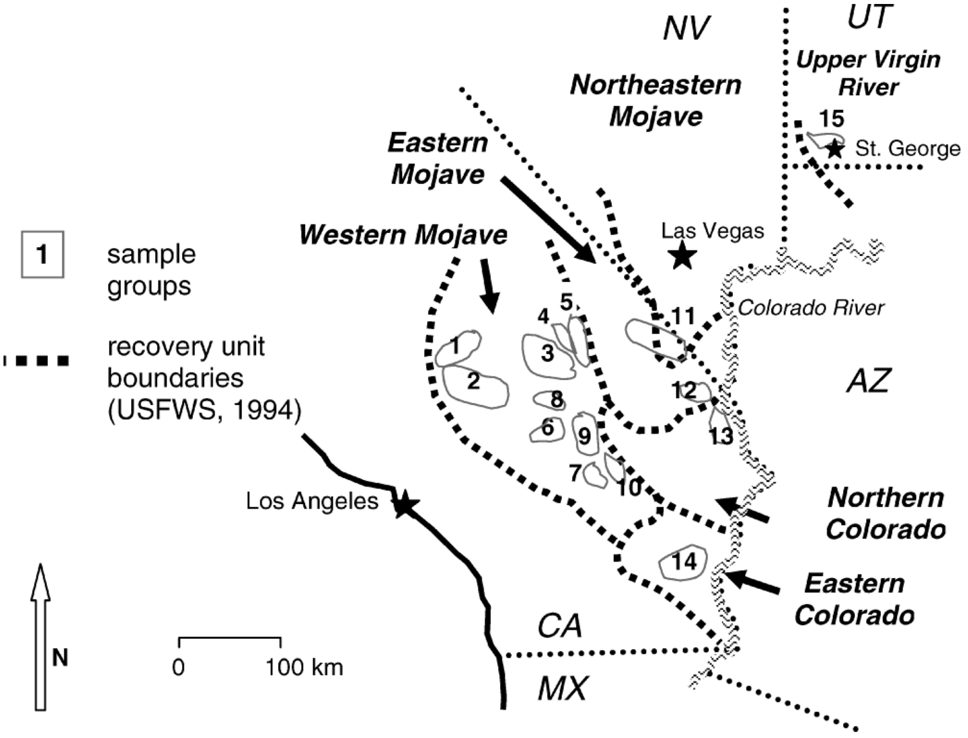

Figure 1. Sample groups and recovery unit boundaries for *Gopherus agassizii* as described in the *Desert Tortoise (Mojave Population) Recovery Plan* (USFWS 1994) and sample sites for this study. Because of their geographic proximity, 3 tortoises from the Eastern Mojave Recovery Unit were combined with 57 tortoises from the Northeastern Mojave Recovery Unit to form sample group 11.

Desert tortoises exhibit substantial differences in morphology (Weinstein and Berry 1987; Germano 1993), physiology (Turner et al. 1986; Wallis et al. 1999; Averill-Murray 2002; Averill-Murray et al. 2002a, 2002b; McLuckie and Fridell 2002), behavior (e.g., Woodbury and Hardy 1948; Burge 1977; Averill-Murray et al. 2002b; Jennings 2002), and genetics (Lamb et al. 1989; Lamb and Lydeard 1994; McLuckie et al. 1999; Lamb and McLuckie 2002) throughout the geographic range in the United States. This variation occurs within and between the Mojave and Sonoran populations.

The authors of the *Recovery Plan* recommended protection of 6 evolutionarily significant units (ESUs) or distinct population segments (DPSs) in 6 "recovery units" (Ryder 1986; Waples 1991, 1998; US Department of the Interior and US Department of Commerce 1996). They noted that the ESUs (or DPSs) consisted of "populations or groups of populations that show significant differentiation in genetics, morphology, ecology or behavior . . . and thus are important components of the evolutionary legacy of *Gopherus agassizii*" (USFWS 1994). They stated that the conservation of all ESUs would help to ensure that "the dynamic process of evolution [in this species] will not be unduly constrained in the future [Waples 1991]" (USFWS 1994). It is important to note that the authors used the phrases ESUs, DPSs, and recovery units synonymously, and their intent was to draw on multiple criteria to delineate units (after Waples 1991, and similar to Crandall et al. 2000). The USFWS also recommended that concepts in the *Recovery Plan* be subjected to hypothesis-testing. In the case of genetics, the limited available mitochondrial deoxyribonucleic acid (mtDNA) data suggested that *G. agassizii* might be composed of more than 1 species, with the Colorado River acting as a boundary in the northern part of the geographic range (Lamb et al. 1989; summarized in Berry et al. 2002).

Since the *Recovery Plan* (USFWS 1994) was published, the fields of population and conservation genetics have advanced rapidly. Numerous new, powerful techniques are now available for processing, statistically analyzing, and interpreting genetic samples (e.g., DeSalle and Amato 2004; Pearse and Crandall 2004; Manel et al. 2005; Allendorf and Luikart 2007). In 1996, the federal government further clarified the Endangered Species policy on DPSs for vertebrates (US Department of the Interior and US Department of Commerce 1996). The academic dialog on the definitions and applicabilities of ESUs, DPSs, and other related concepts, such as management units (MUs), Canadian designatable units (DUs), and adaptive evolutionary conservation has continued to be rigorous and brisk (Crandall et al. 2000; Fraser and Bernatchez 2001; Pearman 2001; Moritz 2002; Green 2005). However, distinct infraspecific populations of American vertebrates, except for salmonid fishes, can currently only receive legal protection as DPSs, not as ESUs.

A factor complicating the genetic study of desert tortoise populations has been human-mediated translocation. The tortoise has received much well-intended attention by governmental agencies and concerned citizens since the 1930s (California Code of Regulations 2007). Thousands of tortoises have been taken into captivity and then released. Still others have been translocated from one area to another in the desert. Commercial harvesting and interstate transportation have been significant.

Our objectives are to contribute to recovery efforts for this species by: 1) characterizing genetic differences in the Mojave populations to determine whether the existing 6 recovery units are genetically distinguishable and, if so, to what extent; 2) evaluating the potential effects of numerous releases and translocations of tortoises on genetic structure; and 3) placing the genetic data in the context of ecological and behavioral differences in desert tortoises to support the conservation of ecological and evolutionary processes.

METHODS

Sample Collection

We salvaged blood from desert tortoises used in research projects on health, disease, and physiology, and through collaboration with other scientists (Henen et al. 1997; Brown et al. 1999; Christopher et al. 1999, 2003; Edwards 2003). Desert tortoises were captured by hand in the field by following federal and state protocols (Averill-Murray 2000; Berry and Christopher 2001). Samples were collected from tortoises ($n = 628$) at 31 study sites that occur within the geographic range where the tortoise is federally listed (USFWS 1990) (Table 1; Fig. 1). We did not include sites from Nevada or the Beaver Dam Slope, Utah. Study sites were in remote areas as well as < 2 km from towns or human habitation. We also obtained mtDNA sequences from 4 *G. agassizii* from the Sonoran Desert of Arizona (Edwards et al. 2003), 1 sample of the bolson tortoise (*Gopherus flavomarginatus*) from a private collection, and 1 sample of the Texas tortoise (*Gopherus berlandieri*) from the Department of Animal Care and Technologies at Arizona State University, Tempe (J. Badman).

About 1 ml whole blood was collected via brachial, jugular, or subcarapacial venipuncture, and the samples were stored on ice or dry ice in (ethylenediamine tetraacetic acid [EDTA]), lithium heparin, or 95% ethanol. Most samples (from health and disease studies) were centrifuged first, the plasma was removed, and the red blood cells were retained and frozen for DNA extraction.

Molecular Techniques

Molecular procedures were conducted at the Genomic Analysis and Technology Core, University of Arizona. Genomic DNA was isolated from blood by overnight lysis with proteinase K at 55°C, followed by a phenol/chloroform extraction and isopropanol/sodium acetate precipitation (Goldberg et al. 2003). The DNA was resuspended in low TE (10 mM Tris-pH 8.0, 0.1 mM EDTA) and diluted to a 5 ng/μL working stock for polymerase chain reaction (PCR) amplifications.

MtDNA Sequencing. — We amplified an ca.1500–base-pair (bp) portion of the nicotinamide adenine dinucleotide dehydrogenase subunit (ND)3, arginine transfer RNA (tRNA) ND4L, and part of the ND4 genes by using primers Nap2 and New Gly (Arévalo et al. 1994; Britten et al. 1997; Edwards 2003). PCR followed Edwards (2003), and the PCR products were purified by using the QIAquick PCR purification kit (Qiagen, Valencia, CA) and were sequenced on an ABI Prism 3700 DNA Analyzer (PE Biosystems, Foster, CA). Internal primers were designed by using Oligo Primer Analysis Software 6.68 (Molecular Biology Insights, Inc, Cascade, CO): Nap2IN 5'AGGCGGTCAATAATGC-TAATC3' and NewGIN 5'TAATAAAACCAGACAAT-GAAAAAC3'. These primers amplified an 1109-bp portion of ND3/ND4, which was aligned and evaluated by using Sequence Navigator 1.0.1 (Applied Biosystems, Inc, Foster, CA).

Nuclear DNA Assessment. — Data gathering was carried out on an ABI Prism 3730 DNA Analyzer (PE Biosystems). All samples were tested for 16 microsatellite loci (Table 2). The loci were PCR amplified in 6 separate multiplex reactions by using 5' fluorescently labeled forward primers. We sequenced selected products for all loci to verify repeat motifs. Repeat motifs were identified by using Sequence Navigator 1.0.1 (Applied Biosystems, Inc). Reliably scored, variable loci were used for analysis.

Analysis

Grouping of Samples. — Sample sizes from each of the 31 study sites ranged from 3 to 74 (Table 1). Study sites were assigned to 1 of 15 sample groups based on location, proximity to nearby sites (≤ 60 km), potential topographic or geographic barriers to movement of tortoises, region of the desert, recovery unit as described in the *Recovery Plan* (Fig. 1), and the need to maintain a minimum sample size for statistical analyses. Thus, the 15 sample groups contained 18–83 tortoises (Table 1). Sample group 11 combined individuals from Ivanpah, California ($n = 57$), which belong to the Northeastern Mojave Recovery Unit, with 3 tortoises from Shadow Valley in the Eastern Mojave Recovery Unit owing to close geographic proximity of the localities. We assigned groups to regions of the Mojave and Colorado deserts by using boundaries similar to those described in Rowlands et al. (1982), and the boundary between the Mojave and Colorado deserts as described in Jaeger (1957), Benson and Darrow (1981), Rowlands et al. (1982), and Turner et al. (1995). For boundaries delineating the northern and eastern regions within the Colorado Desert, we followed the *Recovery Plan* (USFWS 1994; Rowlands 1995a, 1995b).

MtDNA. — We selected 125 tortoises representing all recovery units, including 47 samples from the Northeast-

Table 1. Desert tortoise study sites and sample groupings representing 8 regions for the Mojave population.

Desert region/recovery unit	Study site	No. samples	Group	No. samples in group
Western Mojave	Desert Tortoise Research Natural Area	58	1	62
	Fremont-Valley	4	1	
	Hinkley	12	2	83
	Kramer	3	2	
	Edwards Air Force Base	57	2	
	Fremont-Kramer	11	2	
"Central Mojave"	Superior-Cronese	10	3	19
	Fort Irwin (Goldstone)	9	3	
	Fort Irwin (Tiefort)	31	4	31
	Fort Irwin (Soda Mtns.)	33	5	47
	Fort Irwin (Eastgate 2)	14	5	
"Southern Mojave"	Lucerne Valley	12	6	26
	Ord-Rodman	14	6	
	MCAGCC[a] (Emerson)	9	7	71
	MCAGCC (Sand Hill)	62	7	
	Daggett	74	8	74
	MCAGCC (Lavic Lake)	8	9	27
	MCAGCC (Maumee Mine)	7	9	
	MCAGCC (Sunshine Peak)	12	9	
	MCAGCC (Bullion)	16	10	19
	MCAGCC (Lava)	3	10	
Northeastern Mojave	Ivanpah	34	11	60
	Ivanpah (site 14)	23	11	
	Shadow Valley[b]	3	11	
Eastern Mojave	Fenner	4	12	31
	Goffs	27	12	
Northern Colorado	Chemhuevi	7	13	18
	Upper Ward Valley	11	13	
Eastern Colorado	Chuckwalla	18	14	37
	Chocolate Mtns.	19	14	
Upper Virgin River	near St. George, UT	23	15	23

[a] MCAGCC = Marine Corps Air Ground Combat Center.

[b] Population occurring in the Eastern Mojave Recovery Unit assigned to the Northeastern Mojave sample group for purposes of data analysis owing to geographic proximity.

Table 2. Observed microsatellite motifs in Mojave desert tortoises, *Gopherus agassizii*, compared with that of the originally described species or population.

Locus	Species originally described	Original repeat motif	Observed motif in Mojave population	Range of Mojave alleles	Range of Sonoran alleles
Edwards et al. 2003					
Goag3	*G. agassizii* (Sonoran)	$(\mathrm{CAA})_6$	$(\mathrm{CAA})_6$	6–7	6–9
Goag4	*G. agassizii* (Sonoran)	$(\mathrm{CAA})_{24}$	$\mathrm{CAA})_{24}$	12–32	7–30
Goag5	*G. agassizii* (Sonoran)	$(\mathrm{GAT})_8$	$\mathrm{GACGAA(GAT)_2GACGAA}$	null	6–38
Goag6	*G. agassizii* (Sonoran)	$(\mathrm{TC})_8(\mathrm{AC})_{11}$	$(\mathrm{TC})_8(\mathrm{AC})_{11}$	17-–67	15–52
Goag7	*G. agassizii* (Sonoran)	$(\mathrm{AC})_3(\mathrm{GC})_5(\mathrm{AC})_{11}$	$(\mathrm{AC})_8(\mathrm{AT})_2\mathrm{GC}(\mathrm{AC})_3(\mathrm{GC})_3(\mathrm{AC})_9$	13–28	12–28
Goag32	*G. agassizii* (Sonoran)	$(\mathrm{AC})_6$	$(\mathrm{AC})_6$	6	5–6
Schwartz et al. 2003					
GP26	*Gopherus polyphemus*	$(\mathrm{GT})_{12}$	$(\mathrm{GT})_7$	7	6–9
GP55	*G. polyphemus*	$(\mathrm{GT})_9$	$(\mathrm{GT})_7$	7–30	7–34
GP102	*G. polyphemus*	$(\mathrm{GT})_5(\mathrm{CT})_{13}(\mathrm{CA})_5$	$(\mathrm{TC})_2(\mathrm{TG})_2\mathrm{CG}\ [(\mathrm{TG})_8(\mathrm{TC})_{14}]$[a]	19–42	19–36
GP15	*G. polyphemus*	$(\mathrm{GA})_{15}(\mathrm{GT})_8$	$(\mathrm{GA})_{14}(\mathrm{GT})_{20}$	13–52	13–56
GP19	*G. polyphemus*	$(\mathrm{GT})_9/(\mathrm{GT})_3(\mathrm{GA})_6$	Allele 1; $(\mathrm{GT})_3/(\mathrm{GT})_2\mathrm{GAAA}(\mathrm{GA})_4$ Allele 2; $(\mathrm{GT})_7\mathrm{ATGTATGT}/(\mathrm{GT})_2\mathrm{GAAA}(\mathrm{GA})_5$	11 and 21	6, 11, and 21
GP30	*G. polyphemus*	$(\mathrm{GT})_{13}$	$(\mathrm{GT})_5(\mathrm{CT})(\mathrm{GT})_4$	10–17	5–29
GP81	*G. polyphemus*	$(\mathrm{GT})_{11}(\mathrm{GA})_{10}$	$(\mathrm{GT})_9\mathrm{GACA}(\mathrm{GA})_8$	16–28	18–22
GP61	*G. polyphemus*	$(\mathrm{GT})_{12}$	$(\mathrm{GT})_4\mathrm{AT}(\mathrm{GT})_6$ & $(\mathrm{GT})_{16}$	11–38	9–43
GP96	*G. polyphemus*	$(\mathrm{GA})_{11}$	$(\mathrm{GA})_7$	7	7
FitzSimmons et al. 1995					
Cm58	*Chelonia mydas*	$(\mathrm{CA})_{13}$	$(\mathrm{TA})_5(\mathrm{GA})_3\mathrm{GC}(\mathrm{GT})_3$	12	12–13

[a] Complex repeat; unable to obtain entire sequence.

ern Recovery Unit, and sequenced their mtDNA for a total evidence analysis (Kluge 1989; Ernisse and Kluge 1993) of unique haplotypes only. Unweighted maximum parsimony analyses were performed on potentially informative characters by using PAUP* 4.0b10 (Swofford 2002). Most parsimonious trees were obtained by using the heuristic tree search algorithm with random addition of individuals, 10,000 replicates while retaining minimal trees only and holding 10 trees at each replicate, tree bisection-reconnection branch swapping with the steepest descent, and collapsed zero-length branches. All multistate characters were evaluated as nonadditive (unordered). Nodal consistency was assessed by using nonparametric bootstrap proportions (Felsenstein 1985) and decay analysis (Bremer 1994) performed in PAUP*. Relative nodal support was assessed by using bootstrapping with 10,000 random pseudoreplicates of the data, with each pseudoreplicate being replicated twice.

Bayesian inference was also used to hypothesize matriarchal history (Huelsenbeck and Ronquist 2001; Buckley et al. 2002; Nylander et al. 2004; Ronquist 2004). MrModeltest 2.2 (Nylander 2004) was used to select the best evolutionary model based on the Akaike Information Criterion (Akaike 1974, 1979). Hierarchical likelihood ratio tests (Goldman 1993) compared log-likelihood scores of 56 models. Bayesian inference, conducted by using MRBAYES 3.1.2 (Huelsenbeck and Ronquist 2001), started with random trees. Six Markov chains were used, and the data set was run for 3×10^6 generations. Trees were sampled every 100 generations. Two independent analyses with different starting trees were run and the fluctuating values of likelihood were graphically monitored (Huelsenbeck and Bollback 2001). Log-likelihood scores of sample points were plotted against generation time to establish stationarity (Huelsenbeck and Ronquist 2001). The analysis was a priori required to achieve a split frequency standard deviation of ≤ 0.005. After discarding 25% of the sampled trees as burn-in, the remaining trees were used to generate a 50% majority rule consensus tree.

Nuclear DNA. — We used several methods of analyses to assess gene flow and population differentiation. Each of the methods had different assumptions and relied on different properties of the data, as noted below.

Population Structure. — We used 1) traditional techniques that a priori defined sample groups and 2) an a posteriori genotypic clustering method to analyze population structure. Individuals for which more than 3 loci did not amplify were discarded. Allelic frequency distributions for unique (study site or region restricted) and private alleles ($>$ 5% in a sample group or region) were examined. Loci that exhibited more than 7 alleles were examined by using the log-likelihood-based (G-based) exact test (Goudet et al. 1996) in GENEPOP 3.1 (Raymond and Rousset 1995). A triangular contingency table and a modified version of the Markov-chain random walk algorithm (Guo and Thompson 1992) were used in ARLEQUIN 2.0 (Schneider et al. 2000) to detect significant departures from the Hardy-Weinberg equilibrium (H-W). The multiple tests were not Bonferroni corrected because we looked for trends only and not a precise application of statistical tests. The trends would have remained with a Bonferroni correction but the levels of significance (p-values) would have been raised, possibly to the extent of no significance. Default parameters in GENEPOP and ARLEQUIN were used for all Markov-chain tests and permutations.

Linkage equilibrium is assumed by some statistical tests and, thus, was necessary to confirm. GENEPOP tested for linkage disequilibrium (nonrandom association between loci) among all pairs of loci in the entire sample and within each group by using the method of Garnier-Gere and Dillmann (1992).

Population genetic structure was assessed under nonequilibrium conditions (Pearse and Crandall 2004; Manel et al. 2005). We used STRUCTURE 2.1 (Pritchard et al. 2000) to a priori define cohesive genetic units. Because it does not provide a good measure of genetic structuring in populations that exhibit nonlinear patterns of isolation-by-distance (IBD; Kimura and Weiss 1964; Pritchard et al. 2000), as do Mojave desert tortoises, STRUCTURE was used as a guideline only. An extension to the program by Falush et al. (2003) accounts for correlations between linked loci that arise in admixed populations. We evaluated the 15 sample groups (K populations) with 4 simulations of 500,000 iterations for each K by using the default parameters for an admixture model with a prior mean Φ_{ST} (F_{ST} sensu Weir and Cockerham 1984) of 0.06 (0.05 SD), based on the mean generated from our data set. (We initially also tried the analysis with a lower number of runs by using prior mean Φ_{ST} of 0.01, without a noticeable difference in the outcome.) The best model had the smallest value of K and the largest likelihood values.

To reduce the strongest effects of multilinear IBD, we performed an analysis on the Western Mojave Recovery Unit but first removed the northern- and southernmost samples. The analysis included sample groups 1–10 and used 1,000,000 iterations with a prior mean of Φ_{ST} at 0.01.

Population differentiation was also assessed by using WHICHRUN 4.1 (Banks and Eichert 2000), which calculates the likelihood of a given individual originating from either of 2 or more candidate populations. If the groups identified by STRUCTURE and/or the 6 units hypothesized in the Recovery Plan were distinct and not interconnected by frequent gene flow, then WHICHRUN should assign an individual to its source population with a high likelihood score and assign it to other populations with low scores. Stringency for population allocation used a selection criterion of the log of the odds ratio (LOD) for the 2 most likely source populations. The chance of error is equal to the inverse of this ratio; assignments with a LOD of at least 2 had a ≤ 0.01 chance of error.

Traditional equilibrium-based F-statistics, using analysis of molecular variance (AMOVA) in GENEPOP, were also employed to infer population structure. Inbreeding coefficients (Φ_{IS}; F_{IS} sensu Weir and Cockerham 1984) were calculated for each locus in each sample group. Genetic distances based on pairwise Φ_{ST} were calculated among groups and individuals by using GENEPOP and were visually assessed by producing a multidimensional monotonic scaling plot (MDS) that used the program NTSYS (Exeter Software, NTSYS pc 2.1, Setauket, NY). Goodness of fit was measured by using the Stress test (Kruskal and Wish 1978). Mantel tests obtained from NTSYS assessed correlations between genetic and geographic distances among sample groups. The Φ_{ST} values estimated population structure and gene flow by assuming mutation-drift or migration-drift equilibrium with symmetric migration in both directions for all pairwise combinations of populations. The Φ_{ST} values also assumed an island model that may not be met in desert tortoises, especially because they have experienced recent demographic declines (see Whitlock and McCauley 1999).

Demographic History. — Two very different models assessed historical changes in population density. First, BOTTLENECK (Piry et al. 1999) was used to test for evidence of historical changes in effective population sizes and deviations from equilibrium conditions for each of the sample groups, regions, and the entire population. Populations with recent reductions in effective population size should show an excess of heterozygosity (Cornuet and Luikart 1996; Spencer et al. 2000). Significance of the observed deviations, assuming the infinite alleles model, was determined by the Wilcoxon test as well as the Sign test method of Piry et al. (1999). Second, the M-ratio test of Garza and Williamson (2001) was used to investigate changes in population density and to evaluate bottlenecking, where M is the ratio of the total number of alleles (k) to the overall range in allele size (r). When rare alleles are lost during a population bottleneck, the number of allele size classes is reduced to a greater extent than the range in allele size. Value M is reduced in populations known to have declined in size. In total, 20 populations had the required number of individuals for applying this test. Bottlenecking was assumed to have occurred if M was above the critical value M_C (Garza and Williamson 2001). Congruent findings from the 2 tests would suggest that the results were not biased for any single method or set of assumptions.

Human-Mediated Translocations. — We compiled published and unpublished data and interviewed biologists in state and federal wildlife and land management agencies, then mapped localities of releases or escapes of captive tortoises and translocations of wild tortoises. The results of WHICHRUN assessed the source of an individual tortoise and assignments or misassignments to specific populations. BOTTLENECK, G-based exact tests in GENEPOP, and estimates of inbreeding values (Φ_{IS}) provided information on population trends. Significant deviations from H-W, estimates of recent gene flow and distributions of haplotypes from previously described analyses also provided valuable information.

RESULTS

MtDNA Evaluation. — Estimations of maternal history and population structure were based on *G. agassizii* from the Mojave population and the outgroup taxa (Table 3). All sequences were deposited in GenBank (Accession no. DQ649394–DQ649409).

Seven haplotypes were observed among the 125 *G. agassizii* from the Mojave population (Table 3). Five localities had a single haplotype, and 1 region, the Northeastern Mojave, had 3 sympatric haplotypes, likely a result of the greater extent of sampling at this locality. One haplotype, MOJ-A01, occurred in all but the Northeastern Recovery Unit. Similarly, haplotype MOJ-B01 was common in the Northeastern and Upper Virgin River recovery units but also occurred in low frequency in the Western Mojave and Eastern Colorado recovery units (Table 3). Haplotype MOJ-A02 occurred in 2 nearby localities in the Southern Mojave. MOJ-A03 was found in the nearby Western Mojave and Southern Mojave recovery units. In contrast, haplotypes MOJ-A04 and -B02 occurred at single locations only. Haplotypes within the Mojave population differed at most by 4–5 bp, or only 0.6%, and haplotypes MOJ-B01–03 differed from one another by 1–2 bp only, as did MOJ-A01–04.

Maternal History. — The phylogenetic evaluation was based upon 60 potentially cladistically informative nucleotide positions. In total, 842 nucleotide positions did not vary between the outgroup and ingroup taxa. Autapomorphies occurred at 22 nucleotide sites. The cladistic analysis of the sequences yielded 2 most parsimonious solutions (length = 77 steps, CI = 0.81, RI = 0.95, RC = 0.76). By using *G. flavomarginatus* as the primary outgroup, *G. berlandieri* was resolved as the sister group to all maternal lineages of *G. agassizii*. The consensus trees (Fig. 2) had 2 strongly supported lineages at the base of the tree, one containing Sonoran samples and the other containing samples from the Mojave population. Within the Mojave population, 2 major sublineages were resolved: Haplogroup A, "broadly distributed," and Haplogroup B, Northeastern Mojave. Both lineages contained 1 haplotype that was relatively broadly distributed (Table 3), along with alternative haplotypes. The 2 most basal nodes for *G. agassizii* were strongly supported having bootstrap proportions of 100% and decay indices of 9–10 steps for the Sonoran and Mojave lineages, respectively (Fig. 2). Within the Mojave, Haploclades A and B were only weakly supported; bootstrap proportions = 53%–65% and decay values were 1–2 steps.

When using MrModeltest, the general time reversal plus invariant sites (GTR + G) model was selected for use in the Bayesian inference analysis (–lnL = 2111.7654; K = 9; AIC = 4241.5308). Bayesian inference resulted in

Table 3. The distribution of mitochondrial deoxyribonucleic acid haplotypes from the Mojave desert tortoise, *Gopherus agassizii*.

Desert region/ recovery unit[a]	Group	Haplogroup A				Haplogroup B			Total
		MOJ-A01	MOJ-A02	MOJ-A03	MOJ-A04	MOJ-B01	MOJ-B02	MOJ-B03	
Western Mojave	1	2				1			3
	2	10		1					11
Central Mojave	3	6							6
	5	2							2
Southern Mojave	6	6	2						8
	7	7		1					8
	8	3							3
	9	5	1						6
	10	6							6
Northeastern Mojave	11					40	1	6	47
Eastern Mojave	12	8							8
Northern Colorado	13	3			1				4
Eastern Colorado	14	6				1			7
Upper Virgin River	15	1				4		1	6
Total		65	3	2	1	46	1	7	125

[a] Within the Mojave Desert, 2 major sublineages were resolved: Haplogroup A "broadly distributed", and Haplogroup B, Northeastern Mojave (Fig. 2). The greater relative sampling in the Northeastern Mojave (group 11) reflected an attempt to locate a haplotype from Haplogroup A.

a tree that was identical to the maximum parsimony consensus trees. The Bayesian posterior probabilities were higher than the bootstrap proportions (Fig. 2).

Microsatellite Evaluation. — Of the 16 loci surveyed in 628 desert tortoises (Table 1), 11 were highly variable and informative: Goag03, Goag04, Goag06, Goag07, GP15, GP19, GP30, GP55, GP61, GP81, and GP102. Five loci showed insufficient variation and were excluded from our analyses: GP26, GP96, Cm58, Goag05, and Goag32. For locus Goag03, only 2 study sites exhibited variation: groups 11 and 15 (Northeastern Mojave and the Upper Virgin River recovery units, respectively). For all microsatellite loci used in this study, individual genotypes were summarized by regional groups and are available from the Internet home page of RWM (www.zoo.utoronto.ca/drbob/publications).

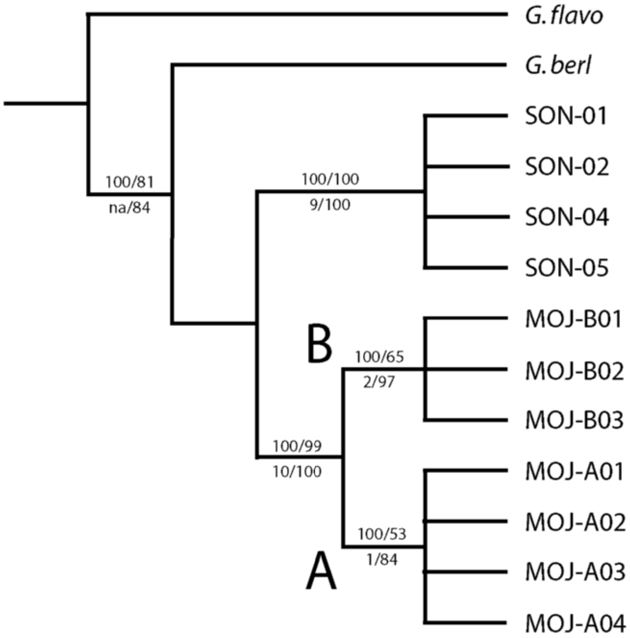

Figure 2. A 50% majority rule consensus tree based on maximum parsimony and Bayesian inference evaluations of the mitochondrial deoxyribonucleic acid sequence data from tortoises, genus *Gopherus*. SON = Sonoran and MOJ = Mojave populations of the desert tortoise (*Gopherus agassizii*) and outgroups G. berl (*G. berlandieri*) and G. flav (*G. flavomarginatus*). Numbers above the branches are given as frequency of resolution in the maximum parsimony evaluation/bootstrap proportions, and below as Bremer support/Bayesian posterior probabilities. Na = not applicable, and letters at nodes denote haplogroup lineages of Mojave populations discussed in text.

Major differences occurred between repeat motifs at some microsatellite loci in *G. agassizii* when compared with species or the population for which the locus was originally isolated, including GP19, GP30, GP61, GP81, and GP102 (Table 2). We were not able to precisely determine the motif for GP102 in *G. agassizii*. Homozygous amplicons were vague in the middle of the sequences, suggesting that 2 alleles were present. Fragment analysis did not allow determination of a heterozygous state (difference in repeat motifs) when amplicon lengths were equal. We did not clone these products to determine the competing sequences but rather made an arbitrary assignment of repeat numbers. Consequently, data for GP102 were not necessarily reflective of all possible heterozygous states.

Locus GP61 exhibited 2 different motif states; alleles having more than 16 repeats had a simple dinucleotide motif, $(GT)_{16+}$. However, alleles scoring in the range of 10–12 repeats had a compound motif, $(GT)_4AT(GT)_6$. As in the Sonoran population (Edwards et al. 2004), heterozygous individuals had both motifs. The simple motif had a greater range of allelic states than the compound motif.

Schwartz et al. (2003) originally described the compound motif for GP19 in *Gopherus polyphemus* as $(GT)_9/(GT)_3(GA)_6$. We found a dramatically derived state

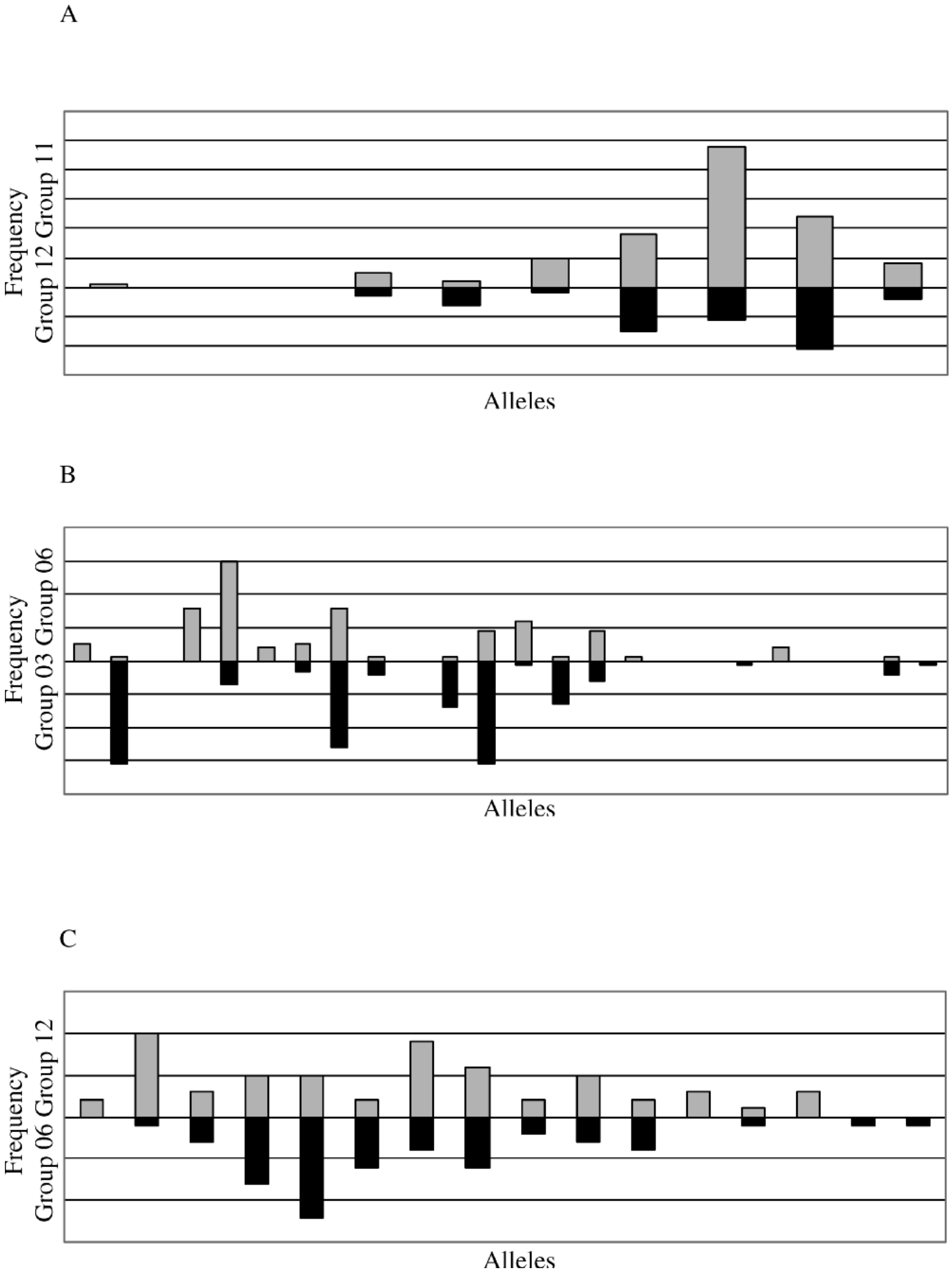

Figure 3. Comparison of allelic frequencies between sample groups of desert tortoises, *Gopherus agassizii*, from the Mojave population by using the G-based exact test for genotypic differentiation. Sample groups refer to Table 1. A: Locus GP81, $p = 0.024$, SE $= 0.002$; B: Locus GP102, $p < 0.001$, SE < 0.001; C: Locus Goag04, $p = 0.031$, SE $= 0.003$.

in our Mojave samples of *G. agassizii*, such that allele 11 sequenced as $(GT)_3/(GT)_2GAAA(GA)_4$ and allele 21 sequenced as $(GT)_7ATGTATGT/(GT)_2GAAA(GA)_5$. Consequently, we could not use analyses that required a stepwise mutation model, such as R_{ST} (Slatkin 1995).

Some dinucleotide loci exhibited imprecise pherograms (e.g., stutter peaks) when the number of repeats exceeded 25. A score of "35" could not be differentiated from "34" or "36". Consequently, pherograms were scored by using a standardized rule set for consistency with error on the conservative side. Loci GP15, GP61, GP102, and Goag06 may have reached the upper limits of our ability to detect repeat numbers, because larger amplicons had very low intensity pherograms. Generally, alleles with more than 55 repeats were not scored, and, thus, we likely missed some alternative alleles.

The distributions of allele size classes for most loci were not normally distributed. Some were highly skewed, and others exhibited multiple peaks (Fig. 3). Unique and private alleles were detected in several sample groups at some of the more variable loci. In some cases, private alleles comprised a high proportion of the alleles observed within a population. For example, sample group 14 had 4 alleles at GP30; the private allele composed 25% of all alleles (Table 4) but it occurred at a frequency of < 5%.

Table 4. Distribution of unique and private alleles in 15 sample groups (summarized in Table 1) of desert tortoises from the Mojave population.[a]

Sample	GP61			GP19			GP102			GP30			GP55			GP15			GP81			Goag4			Goag06			Goag7			Goag3		
group	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%
1	14			2			7			9	1	11	9			17			7	2	29	16			26			5			1		
2	15			2			14			8	1	13	8	1	13	24	1(1)	4.2	5			17	1	5.9	22			4			1		
3	9			2			9			5			8	1	13	15			5			13			16			4			1		
4	11			2			11			7			11			14			6			12			19			4			1		
5	13			2			11			7	1	14	12	1	8.3	16			5			15			21			5			1		
6	10			2			10			4			6			9			6			13			18			4			1		
7	16			2			13	1	7.7	8	2	25	7			21			7			12			21			4			1		
8	14			2			15			7			11			20	1	5	7	1	14	11			33			5			1		
9	11			2			12			6	1	17	7	1(1)	14	10			7			12			22			5			1		
10	13			2			7	1(1)	14.3	4			7			14	1	7.1	7			9			14			4			1		
11	15			2			16	1	6.3	8			6			19			8	1	13	16			19			6			2		
12	18			2			12			9			7			15			7			14			15	1	6.7	4			1		
13	13	1	7.7	2			12			10	2(1)	20	5			14			7			11	1	9.1	14			5			1		
14	15	1(1)	6.7	2			12	1(1)	8.3	4	1	25	9			13			6			11	1(1)	9.1	21			5			1		
15	11			1			12	1(1)	8.3	7			3			15			5			10			15			3			2		
Total	27			2			24			21			17			37			11			22			49			5			2		

[a] T = total number of allelic states observed in a sample group; U = number of alleles unique to the sample group; parenthetic values are the number of unique alleles that occur at a frequency > 5% (private alleles) in a sample group relative to the total number of alleles; % = the percentage of alleles that are unique in a sample group [(U/T) × 100]. No private alleles in a population occurred at a frequency > 8%.

The frequency of occurrence for the relatively rare, private allele was always ≤ 8%.

Most sample group pairwise comparisons between distributions of allelic frequencies (Fig. 3) were found to be significantly different by the G-based Exact test (Goudet et al. 1996). Three sample groups deviated from H-W in exhibiting a greater number of heterozygotes than expected (Table 5). By using a 5% cutoff, about 1 deviation is expected for each locus, except for Goag3. Three loci showed excessive deviations from expectations in the form of heterozygote deficiencies: GP30, G81, and Goag06. In total, 24.5% of the data points showed deviations from H-W, with 8.6% owing to Goag06 alone (Table 5).

Garnier-Gere's and Dillmann's (1992) test rejected the null hypothesis for linkage disequilibrium (equilibrium for locus pairs) for 45 (of 165) locus pairs within 15 sample groups. Nine sample groups had a percentage of total pairwise comparisons with p-values > 0.05 (range 0.0%–26.7%). However, locus pairs did not consistently exhibit disequilibrium among groups.

Bayesian likelihood values for all runs by using STRUCTURE typically stabilized after 50,000–100,000 iterations after burn-in. The analyses obtained the lowest average Ln for 6 subpopulations (Table 6). These subpopulations were concordant with the recommendations in the *Recovery Plan*. Because substantial differentiation was observed in the Western Mojave Recovery Unit, as revealed by Φ_{ST} values, we removed populations 11–15 and performed a new analysis to reduce the affects of IBD. This analysis suggested that the current Western Mojave Recovery Unit supported 4 subpopulations (Table 6): sample groups 1–2, 3–5, 8, and 6–7 plus 9–10 (Fig. 4).

A 2-dimensional, monotonic MDS plot displayed population differentiation among sample groups (Fig. 5). It had a stress of 1.39, a fair to good fit by Kruskal's and Wish's (1978) index. The 15 sample groups clustered complementary to their geographic proximities, as anticipated when assuming gene flow. Geographically distant sample groups 11 and 15 were noticeably separated from the other groups.

Population assignment tests correctly placed the majority of individuals back to their sample groups with high stringency (Table 7). Individuals not assigned to a sample group were frequently assigned to a geographically nearby group or to one within the same region. Geographically proximate groups 12 and 13 occurred near the boundary of 2 desert regions, the eastern Mojave Desert and northern Colorado Desert (Fig. 1). The population assignment evaluations had difficulty distinguishing individuals between these 2 recovery units. Whereas, 80% of the samples from group 11 were correctly assigned, only 48% of 31 samples from group 12 were correctly assigned. However, 87% of tortoises from group 12 were correctly assigned to groups 12 and 13 combined, indicating that, in this case, geographic proximity was a better predictor of genetic structuring

Table 5. Summary of deviation from Hardy-Weinberg expectations for 11 variable microsatellite loci and 15 sample groups of the desert tortoise, *Gopherus agassizii.* Sample groups refer to Table 1.

Locus	No. comparisons	No. heterozygote excess	No. heterozygote deficiency	Range in no. of repeats
GP61	15	0	2	11–38
GP19	14	0	0	11–21
GP102	15	1	1	19–42
GP30	15	0	7	10–17
GP55	15	0	3	7–30
GP15	15	0	2	13–52
GP81	15	0	6	16–28
Goag4	15	1	0	12–32
Goag06	15	0	13	17–67
Goag7	15	1	0	13–28
Goag3	2	0	0	6–7

than recovery unit. A similar trend was discovered for tortoises in group 13.

When sample groups were combined to reflect current recovery units, and when sample groups 12 and 13 were combined, assignment scores of $\geq 80\%$ were obtained (Table 7). For the Western Mojave Recovery Unit, we deleted geographically distant sample groups (1, 2, 11–15) and re(-)ran the assignment test. We combined samples 3–5 and samples 6–10, because they had higher proportions of misassigned individuals than all other units (Table 7). Although not given in Table 7, the percentage of individuals correctly assigned to the proposed Central Mojave (samples 3–5) and Southern Mojave (samples 6–10) recovery units combined was 52% each, with 24% being assigned to the combined unit as the second most likely assignment and 13% assigned to the adjacent Western Mojave Recovery Unit.

Finally, we combined the sample groups to reflect geographic regions, which reflected the current recovery units (Table 7). This treatment recognized variation within the Western Mojave Recovery Unit. In total, 8 regions were identified. Assignment scores ranged from 59.6% to 95.7%. The more fine-grained analyses, those that included a greater number of subdivisions, yielded lower assignment scores.

Geographic substructuring was further assessed by breaking and recombining specific units. The assignment tests produced 96%–98% accuracy when the distribution of tortoises was divided into 2 groups: Northeast (11, 15) and Central (1–10, 12–14), respectively. When geographically proximate groups were split and recombined, the assignment tests invariably decreased, some to less than 50% (sample groups 2, 6, and 8).

The hierarchical analysis of molecular variance indicated the absence of panmixia; significant genetic structuring was discovered. The AMOVA revealed that 93.9% ($p < 0.001$) of the observed variation was partitioned among individuals within sample groups ($\Phi_{IT} = 0.939$), whereas only 6.1% of the variation was among the sample groups ($\Phi_{ST} = 0.061$, $p < 0.001$). The positive significant correlations between genetic distance (pairwise Φ_{ST}) and geographic distance accounted for approximately 65% of the observed variation (Mantel test; $r^2 = 0.646$, $p = 0.002$).

By using BOTTLENECK, we detected a significant excess in heterozygosity in 2 sample groups, 11 and 15, the Northeastern Mojave and Upper Virgin River recovery units. The Wilcoxon Test with the (infinite alleles model [IAM]) detected an excess in both groups but the Sign Test (IAM) method of Piry et al. (1999) identified group 15 only. No deficit or excess in heterozygosity was detected when the data for all groups were combined. All sample sets fit the expected beta distribution (Cornuet and Luikart 1996), thus providing no evidence for bottlenecking. By using the method of Garza and Williamson (2001) to detect potential reduction in population size, all values of M fell above the critical value M_C. However, the results may not be reliable, because this test assumed stepwise mutation.

Human-Mediated Translocations. — Native Americans undoubtedly moved desert tortoises from one place to another (as implied in Schneider and Everson 1989). The distances were probably limited, except for annual gatherings for mourning ceremonies (i.e., Las Vegas Band, Southern Paiute: Kelly, no date) and the result may have been death for the tortoises.

Throughout the 20th century, tortoises were captured for domestic pets and were translocated for various purposes. Captive tortoises currently or formerly kept by residents of desert communities often escape or are deliberately released into adjacent desert lands. The sources of the captives may or may not be local relative to the point of escape or release. Escaped captives are so common that a publication gives actions to take when a former captive is found (Berry and Duck, 2006). Captives have been observed wandering within city limits or nearby in Ridgecrest, Barstow, Ft. Irwin, Victorville, and Twentynine Palms in the Western Mojave Recovery Unit; Needles in the Eastern Mojave Recovery Unit; Las Vegas in the Northeastern Mojave Recovery Unit; and St. George in the Upper Virgin River Recovery Unit. Tortoises are often taken to or released at protected areas such as parks and Natural Areas (Howland 1989; Ginn 1990; Jennings 1991; Connor and Kaur 2004).

Thousands of tortoises were released in the southwestern deserts by humane societies, California Department of Fish and Game, Nevada Department of Wildlife Resources, Utah Division of Wildlife Resources, State and National Park personnel, academicians and others (Fig. 6). Data are limited before the 1960s, but releases were documented for California and Utah (Hardy 1945; Woodbury and Hardy 1948; Jaeger 1950, 1955). Woodbury and Hardy (1948) surveyed Beaver Dam Slope, Utah (Northeastern Mojave Recovery Unit) for tortoises between 1936 and 1946. At least 6.1% of 281 tortoises found showed signs of previous captivity. Releases also occurred in the

Table 6. Inferred population structure obtained from the software program STRUCTURE 2.1 for all samples, and for a subset of samples from the current Western Mojave Recovery Unit (sample groups 1–10).[a]

All samples ($n = 628$)

	Ln (variance below)				
K	Run 1	Run 2	Run 3	Run 4	Average Ln
1	–25,140.5	–25,144.0	–25,143.6	–25,143.3	–25,142.9
	99.7	106.1	106	105.8	
2	–24,362.2	–24,360.6	–24,360.8	–24,361.2	–24,361.2
	463.9	460.7	462.6	463.3	
3	–23,644.7	–23,646.2	–23,647.9	–23,648.6	–23,646.9
	568.4	570.5	572.8	574.9	
4	–23,283.3	–23,275.4	–23,269.5	–23,272.6	–23,275.2
	827.5	810.6	800.5	804.8	
5	–23,134.7	–23,038.1	–23,030.7	–23,042.5	–23,061.5
	1049.5	1056.0	1041.2	1062.6	
6	–22,881.4	–22,886.7	–22,883.4	–22,893.2	–22,886.2
	1249.2	1260.3	1251.2	1275.1	
7	–23,042.2	–22,840.3	–24,213.8	–24,745.5	–23,710.5
	1921.8	1521.7	4220.5	5220.9	
8	–22,901.4	–23,454.5	–23,144.8	–22,964.3	–23,116.3
	1712.3	3043.6	2204.3	1858.5	
9	–23,538.9	–24,007.6	–22,951.0	–23,041.1	–23,384.7
	3494.4	4412.3	2335.7	2230.9	
10	–22,857.7	–24,696.7	–22,900.7	–22,900.7	–23,339.0
	2208.1	5872.7	2262.5	2280.9	
11	–23,305.8	–24,272.3	–24,176.7	–24,377.2	–24,033.0
	3318.1	5406.3	5027.1	5490.7	
12	–23,236.8	–24,848.4	–23,590.5	–34,317.7	–26,498.4
	3426.8	6666.9	4129.0	25,502.9	
13	–24,346.5	–23,339.1	–34,657.2	–28,975.2	–27,829.5
	5879.4	3820.1	26,339.3	15,064.1	
14	–31,546.3	–560,553.8	–31,303.2	–24,971.2	–162,093.6
	20,362.5	1,077,674.6	19,809.4	7242.0	
15	–133,340.8	–28,256.8	–27,197.9	–41,616.9	–57,603.1
	223,973.3	13,936.0	11,869.1	40,664.7	

Western Mojave samples ($n = 459$)

K	Run 1	Run 2	Run 3	Run 4	Average Ln
1	–17,343.6	–17,342.7	–17,338.4	–17,339.0	–17,340.9
	99.8	97.2	90.7	90.8	
2	–16,870.6	–16,871.0	–16,870.0	–16,873.2	–16,871.2
	405.0	406.7	405.5	411.5	
3	–16,968.7	–16,715.6	–16,722.3	–16,626.4	–16,758.3
	1218.3	693.6	847.8	657.2	
4	–16,438.7	–16,434.3	–16,432.9	–16,438.4	–16,436.1
	874.5	863.0	860.4	871.3	
5	–16,380.9	–16,404.5	–16,419.0	–18,206.9	–16,852.8
	1068.9	1114.4	1143.6	4629.7	
6	–16,742.5	–16,392.3	–16,418.5	–17,106.1	–16,664.9
	1876.6	1163.9	1217.5	2750.5	
7	–16,778.8	–17,811.3	–16,450.6	–18,021.6	–17,265.6
	2430.1	4440.4	1540.5	4871.7	
8	–16,343.7	–18,314.1	–18,520.9	–16,417.4	–17,399.0
	1837.0	5698.8	5924.8	1746.6	
9	–20,559.6	–17,456.7	–16,346.8	–19,067.6	–18,357.7
	10,289.0	4207.3	1842.1	7354.0	
10	–18,184.4	–406,665.0	–19,777.8	–21,971.6	–116,649.7
	5770.3	780,420.0	8955.7	13,321.4	

[a] K = the number of populations set as the a priori for the simulation; Ln = the log likelihood of the data averaged over all iterations after burn-in (with variance reported below); and the average Ln for all 4 runs for a given simulation. (For all simulations: 250,000 iterations per run with a burn-in of 5000).

vicinity of St. George and the Upper Virgin River Recovery Unit (Hardy 1945).

From the late 1960s to the mid 1970s, the California Department of Fish and Game sponsored numerous captive releases and kept records for > 800 individuals (Fig. 6). Their last official release was the rehabilitation experiment at the Quarterway and Halfway Houses in the Living Desert Reserve and Ft. Soda, respectively, in the late 1970s. Among 200 tortoises initially in the program, 30 survived, only to be moved to private lands in the Antelope Valley (Cook et al. 1978; Weber et al. 1979; Cook 1983).

In Nevada, the first documented releases of captive tortoises occurred on the Desert Game Range in 1973 (B.L. Burge, *pers. comm.*, December 2005; Fig. 6). In the late 1970s and early 1980s, employees of the Nevada

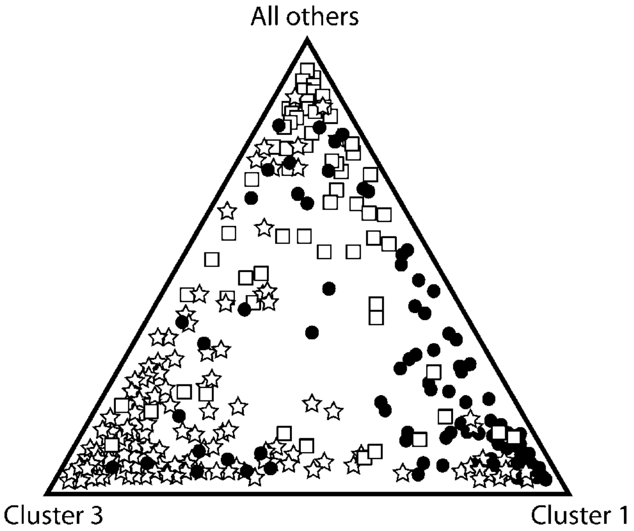

Figure 4. Triangle plot of the estimated membership coefficients for each individual in the Western Mojave Recovery Unit. Symbols correspond to sampling groups (given in Table 1) when the number of populations (K) is K = 3: circles = sample groups 1 and 2, squares = sample groups 3–5, stars = sample groups 6–10. Note the general clustering in the corners of each group and the overall pattern of admixture (gene flow). The cluster of stars in the circle samples depicts individuals mostly from Group 8, which is geographically the most proximate to the circle sample group.

Department of Wildlife Resources released hundreds of captive tortoises onto desert lands (R.J. Turner, *pers. comm.*, December 2005).

State and federal agencies approved the release of numerous captive and wild tortoises in 1997 at a long-term release site in southern Nevada (Field 1999). Additional translocation projects occurred throughout Nevada between 1990 and 2005 (Corn 1991; Nussear 2004; Charles Le Bar, *pers. comm.*, December 2005).

Between 1973 and 1983, the Utah Division of Wildlife Resources released at least 195 captive tortoises on Beaver Dam Slope (Coffeen, *pers. comm.*, December 2005; Coffeen 1984, 1985). In 1980, a general survey conducted throughout 324 km^2 of the area revealed that 21.9% of 105 located tortoises were marked captives (Minden 1980). Tortoises were also released on the historical Woodbury and Hardy (1948) site; when the study site was surveyed in 1981, 23.3% of the 73 tortoises observed were marked captives (Minden and Keller 1981). In the mid to late 1980s, captive tortoises were released in the Upper Virgin River Recovery Unit at Grapevine Pass and Red Cliffs Recreation Area (Coffeen 1986); 71 captive tortoises were also released at Hurricane Cinder Knolls (McLuckie, unpubl. data, 2006).

Evidence exists of a substantial transfer of tortoises from the western Mojave Desert in California to Utah. In April of 1970, 2 wardens arrested a commercial collector who claimed to have taken thousands of tortoises from the Western Mojave Recovery Unit of California between the 1960s and April 1970 and sold them commercially in Salt Lake City, Utah (Berry 1984). Some of these tortoises may have been released on the Beaver Dam Slope and north of St. George in the 1970s and early 1980s in what are now the Northeastern Mojave and Upper Virgin River recovery units.

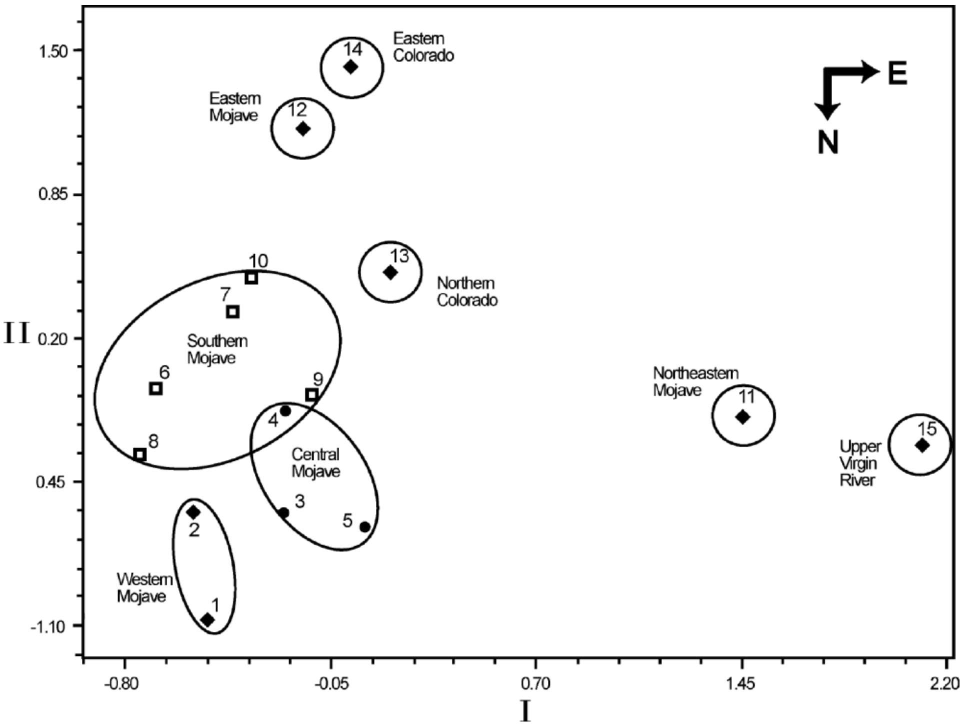

Figure 5. A 2-dimensional scaling plot of genetic distances (Φ_{ST}) for 15 sample groups of desert tortoises, *Gopherus agassizii*, from the Mojave population. Open squares and solid circles indicate samples from the southern and central Mojave Deserts, respectively.

Table 7. Population assignment tests for desert tortoises from the Mojave population and 8 desert regions or recovery units. The initial evaluation treated all 15 sample groups separately. The second treatment combined tortoises into units reflecting the recovery units recommended in the 1994 *Recovery Plan* except for combining sample groups 12 and 13. The third treatment considered populations on the basis of existing and proposed recovery units.

Sample group	No. samples	No. correctly assigned	% Correctly assigned	% With LOD > 2[a]	No. assigned to same region or neighboring group	% Assigned to same region
1	62	42	67.7	58.1	8	80.6
2	83	26	31.3	19.3	16	50.6
3	19	10	52.6	47.4	3	68.4
4	31	11	35.5	22.6	11	71.0
5	47	25	53.2	51.1	12	78.7
6	26	12	46.2	42.3	11	88.5
7	71	20	28.2	19.7	37	80.3
8	74	34	45.9	35.1	13	63.5
9	27	8	29.6	14.8	14	81.5
10	19	10	52.6	52.6	5	78.9
11	60	48	80.0	78.3	0	80.0
12	31	15	48.4	38.7	12 (to group 13)	87.1
13	18	10	55.6	27.8	3 (to group 12)	72.2
14	37	28	75.7	59.5	0	75.7
15	23	22	95.7	91.3	0	95.7
Combined groups						
15	23	23	100			
11	60	51	83.3	10		
12, 13	49	41	81.6	8.2		
14	37	35	91.9	5.4		
1–10	459	377	80	8.5		
Region						
Western Mojave	164	139	84.8			
Central Mojave	97	66	68.0			
Southern Mojave	198	118	59.6			
Northeastern Mojave	60	49	81.7			
Eastern Mojave	31	17	54.8			
Northern Colorado	18	13	72.2			
Eastern Colorado	37	33	89.2			
Upper Virgin River	23	22	95.7			

[a] LOD = log of the odds ratio.

DISCUSSION

Maternal History. — Two distinctive maternal lineages exist, one associated with the Sonoran population in Arizona and the other with the Mojave population. By using *G. flavomarginatus* as the outgroup, the sister group to *G. agassizii* was *G. berlandieri* (Fig. 2). This resolution differed from that of Lamb et al. (1989). Rooting with the same outgroup, they found that the Sonoran *G. agassizii* was the sister group of *G. berlandieri* and exclusive of the Mojave population. The difference could have resulted from several factors. Lamb et al. (1989) evaluated restriction fragment length polymorphisms, and we used more precise sequences. They also had greater taxonomic and geographic sampling. Although we might have reached a similar conclusion if we had used the same coverage, this was unlikely. The difference likely resulted from their use of presence/absence coding of nonhomologous fragment lengths.

Within Mojave population samples, little differentiation occurred among the 7 haplotypes (Fig. 2). Two primary maternal sublineages occur in the Mojave population, but the minor level of differentiation was not indicative of taxonomic differentiation. In contrast, the substantial sequence differentiation between Mojave and Sonoran (Arizona) populations is consistent with the hypothesis that *G. agassizii* consists of more than one species (Berry et al. 2002).

Descriptive Statistics of Microsatellite nuclear DNA (nDNA). — The motif differences in interspecies amplification of microsatellite loci indicated that evaluation of data required species-specific and even population-specific sequence information. Loci amplified between species (and within species too; Estoup et al. 2002.) did not necessarily follow assumptions of the stepwise mutation model.

Deviations from H-W could have several sources. Excess of homozygotes at some loci (e.g., Goag06) could have resulted from nonamplifying alleles, as a consequence of motif anomalies. Translocations of tortoises throughout the Mojave population also might have contributed to the excess of heterozygosity. For cases of heterozygotic deficit, ambiguities associated with high numbers of repeats might have artificially inflated the number of observed homozygotes or elevated Φ_{IS} values if translocated tortoises had very different allele frequencies

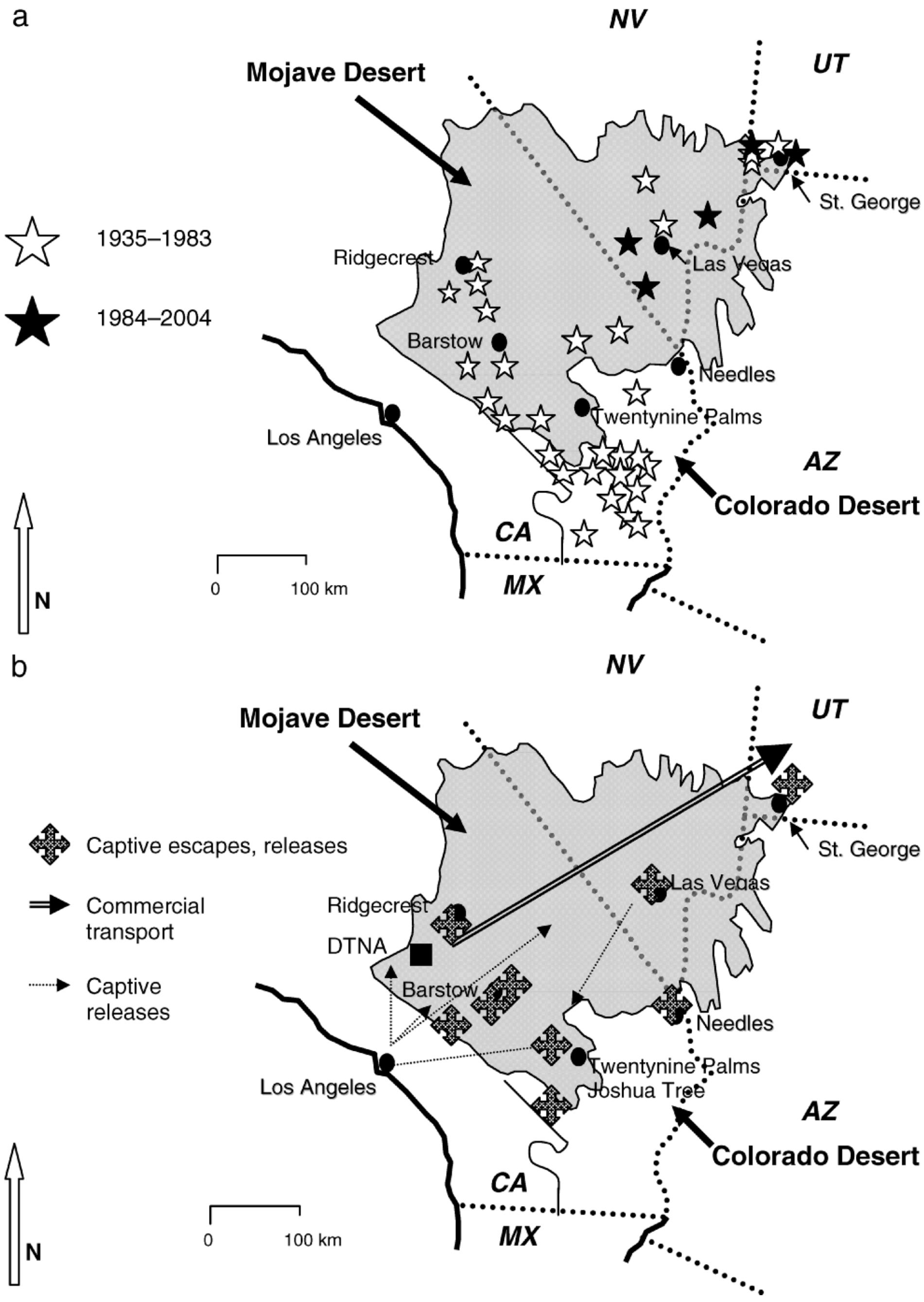

Figure 6. (a) Locations of captive desert tortoises, *Gopherus agassizii*, released by the California Department of Fish and Game, Nevada Department of Wildlife, Utah Division of Wildlife Resources or by others, as described in government reports and university theses and dissertations. The shaded area indicates the limit of the Mojave Desert. (b) Locations of areas where captives escaped or were released outside of desert towns. Tortoises were taken from the Los Angeles basin and released at places such as the Desert Tortoise Research Natural Area (DTNA) or Joshua Tree National Park. There were also large-scale commercial transfers of tortoises.

(a Wahlund effect, lower than expected heterozygosity owing to population substructuring). Technical difficulties of accurately scoring heterozygotes with high numbers of repeats surely contributed to the estimates of heterozygosity deficiencies at Goag06 and possibly at other loci (Table 5). Unfortunately, the proportions of misscored loci cannot be accurately partitioned from the data set to examine for a Wahlund effect (e.g., Chapuis and Estoup 2007).

In total, 24.5% of the data points showed deviations from H-W in the form of heterozygote deficiencies (Table 5). Such deviations may not significantly affect our conclusions. Dankin and Avise (2004) showed that 20% of the data points can deviate from H-W, without affecting the accurate determination of parentage. Empirically, the great correspondence between the results of the microsatellite analyses and ecological boundaries supports our assumption of the utility of the data irrespective of their deviations from H-W expectations.

For tortoises, IBD (isolation-by-distance) affected the probability of individuals mating with one another and violated the assumption of panmixia for statistical tests. Significant pairwise associations of some loci (Table 5) may have reflected an absence of panmixia (i.e., a Wahlund effect), mating systems or problems in resolving alleles. However, because significant linkage disequilibrium was not observed in all groupings, this explanation was unlikely. The greater than expected deviations from H-W were strongly paralleled by Φ_{IS} values. Some deviations from H-W owed to technical constraints (e.g., Goag06), but this was unlikely for other loci (e.g., GP30, GP81). Some positive inbreeding coefficients and departures from H-W may have been because of population structure. However, inbreeding was unlikely to have occurred because most loci did not have significant Φ_{IS} values within a sample group.

Gene Flow. — Genetic structuring was strongly associated with geography (Slatkin and Maddison 1990), IBD, and the limited dispersion of individual tortoises (Mantel test; $r^2 = 0.646$, $p = 0.002$). The results of the AMOVA indicated the absence of panmixia. IBD was also reported by Britten et al. (1997) for allozyme and mtDNA data, and by Edwards et al. (2004) for Sonoran tortoises. Microsatellite variability was greater within than among sample groups, suggesting that the Mojave metapopulation was relatively homogeneous, i.e., the common alleles were broadly distributed. Gene flow likely occurred throughout populations in California, at least until the recent proliferation of anthropogenic barriers. The distribution of low-frequency, unique microsatellite alleles supported the hypothesis that the genetic structure resulted from gene flow and not common ancestry. Indeed, Edwards et al. (2004) noted that desert tortoises were ideal organisms for applying the IBD model, because they are distributed across the landscape in patches, and the difficulty of dispersion is a function of geography.

Bottlenecking. — The excess of heterozygosity in samples from the Northeastern Mojave and Upper Virgin River recovery units could have resulted from recent bottlenecking. However, this possibility was not supported by the ratio of the total number of alleles to the overall range in allele size. Population declines in the Northeastern Mojave and Upper Virgin River recovery units have been well documented in recent years (USFWS 1980; Minden and Keller 1981; Fridell and Coffeen 1993; McLuckie et al. 2004). Although other regions also experienced population declines (Berry and Medica 1995; Brown et al. 1999; Christopher et al. 2003), they did not show genetic evidence of bottlenecks. This inconsistency may have been because of at least 4 factors. First, our samples were collected over 10 years and this could have precluded the effects of recent declines. Second, the time frame for sampling may have been too short for observing a shift in heterozygosity for a long-lived species with a long generation time. Garrigan and Hedrick (2003) reported that 5–10 generations were required to genetically detect bottlenecks. Moreover, Dinerstein and McCracken (1990) did not see bottleneck effects in the greater one-horned rhinoceros by using microsatellite DNA, despite well-documented evidence. Consequently, conclusions on the genetic structure of populations should not be based on molecular evidence alone but should accompany field observations. Third, polyandry, if common, and especially when combined with sperm storage, could have increased the effective population size (Sugg and Chesser 1994). Sperm storage for up to 3 years has been documented in the desert tortoise (Palmer et al. 1998) and anecdotal evidence suggests that it may occur for much longer. (One isolated captive female tortoise produced viable clutches for 15 years after her last known association with a male tortoise; P. Gould Glasco, *pers. comm.*, May 2006.) A controlled investigation of polyandry in the western Mojave Desert found that all females produced polyandrous clutches over a period of 2 years (Murphy, Edwards, Bratton, and Hagen, in prep.). And fourth, the observed increase in heterozygosity in the Northeastern Mojave and Upper Virgin River recovery units may also be a reflection of translocated tortoises. The translocation of gravid females or those that were storing sperm would serve to compound the possible explanations for excess heterozygosity.

Human-Mediated Translocations. — Translocations and releases of animals, especially if uninformed, can have negative genetic consequences (Allendorf and Luikart 2007). The historical releases and translocations of tortoises could have affected our results in the form of deviations from the H-W, increased heterozygosity and estimates of recent gene flow, anomalous distributions of some haplotypes, and increased Φ_{IS} values (through a Wahlund effect). The geographically disjunct occurrence of some haplotypes (MOJ-A01 with -B01 and -B03 in the Upper Virgin River; Table 3) could be caused by translocations. Because the widespread MOJ-A01 haplotype was absent in our initial survey of 7 tortoises in the Northeastern Recovery Unit only, we sequenced 40 additional samples: in total, 40 were MOJ-B01, 6 were MOJ-B03, and 1 was MOJ-B02. Because MOJ-A01 was absent from the Northeastern Recovery Unit, its presence in Upper Virgin River Recovery Unit was likely because of relocated tortoises. Our samples from the Northeastern Mojave were taken from relatively remote areas where the releases of captives were less likely.

Several other incidences of geographic mixing are evident: MOJ-B01 is geographically and genealogically associated with other members of Haplogroup B, but it also occurs in sympatry with Haplotypes MOJ-A01 (Haplogroup A) in the Western Mojave Recovery Unit (Table 3), specifically at the Interpretive Center at the Desert Tortoise Research Natural Area. This finding is concordant with documentation of multiple captive tortoise releases at the Natural Area (Howland 1989; Ginn

1990; Jennings 1991; Connor and Kaur 2004). Haplotype MOJ-B01 also occurs with MOJ-A01 in the Eastern Colorado Recovery Unit. Very long distance dispersion is the alternative explanation for the widespread occurrence of some haplotypes. Given the extent of documented translocations, the dispersion hypothesis is unlikely, particularly because our data lack other evidence of population expansion or recent ancestry.

Translocated tortoises could compromise the genetic integrity of a population by disruption to coadapted gene complexes in local environments or loss of fitness through outbreeding depression. In particular, Beaver Dam Slope, Utah, has a high frequency of released captive tortoises (Woodbury and Hardy 1948, Minden 1980, Minden and Keller 1981). Although we do not have genetic samples from this area, the excess of heterozygotes in the adjacent Upper Virgin River and Northeastern Mojave recovery units, in the absence of a decrease in the ratio of the total number of alleles to the overall range in allele size, could reflect first- or second-generation offspring from translocated tortoises. A similar problem may exist at the Desert Tortoise Research Natural Area and Joshua Tree National Park in the Western Mojave Recovery Unit. Outbreeding depression can lead to reduced fitness via disease in hybrid populations (Goldberg et al. 2005, Allendorf and Luikart 2007). The high levels of assignments of tortoises to the correct region (Table 7) indicate that, in some cases, survival rates of released tortoises may be low, e.g., the early California reintroduction experiments (Cook et al. 1978; Cook 1983; Weber et al. 1979).

Regional Differentiation. — The STRUCTURE analysis identified from 5 to 8 genetically structured units. These findings support the hypothesis of population structure in the *Recovery Plan* and the Desert Wildlife Management Units described in the Western Mojave Recovery Unit. When considering the close geographic proximity of some of our sample groups (e.g., groups 12 and 13), this result was consistent with our assumption that the Mojave population is genetically structured and that these genetic data were informative for designating recovery units. Sample group 8 may have the most admixture between the "Central" and "Southern" areas of the Western Mojave Recovery Unit. This subanalysis suggested that the Western Mojave Recovery Unit could be subdivided into at least 3 geographic groups. Although STRUCTURE is not a good measure of structure in populations that exhibit nonlinear patterns of IBD (Pritchard et al. 2000), the findings were congruent with the *Recovery Plan* and natural barriers to gene flow. Thus, we used these results as evidence for the assessment of recovery units.

The null hypothesis of a single, homogeneous, panmictic Mojave population was rejected. Although most alleles were broadly distributed, most sample groups significantly differed from one another in allelic frequencies (Table 7). Because the G-based exact test is sensitive to different sample sizes, as in our data, the imbalance in samples might have accounted for the high number of significant differences. However, this does not appear to be true. Most individuals ($> 80\%$) were reassigned (Table 7) back to their sample group. The accuracy of the assignments implies genetic divergence.

The population assignment was viewed as a conservative result. Our data set was limited to 11 variable microsatellite loci only. Additional loci would have likely increased the accuracy of the assignments and the distinctiveness of each recovery unit.

Congruent patterns of genetic differentiation from different regions or taxa lend credence to conclusions. Comparatively, desert tortoises from Mojave and Sonoran populations had almost identical genetic structuring at local and regional levels. The AMOVA of microsatellites from the Sonoran population revealed that 96.3% ($p < 0.001$) of the diversity occurred in individuals within study sites ($\Phi_{IT} = 0.963$), whereas only 3.7% ($p < 0.001$) of the variation was among sites ($\Phi_{ST} = 0.037$) (Edwards et al. 2004). The same result occurred in a geographically equivalent sized subset of our data; $\Phi_{ST} = 0.037$ ($p < 0.001$). In both studies, a significant positive correlation occurred between genetic distance (pairwise Φ_{ST}) and geographic distance.

Recovery Units Revisited

The authors of the *Recovery Plan* proposed 6 recovery units to capture the known genetic, morphological, ecological, and behavioral diversity in desert tortoises as of 1993 (USFWS 1994). Their original objectives agree with the views of Crandall et al. (2000), specifically to preserve the options for adaptive diversity and evolutionary processes, maintain a network of populations, reduce the likelihood of further contraction of the geographic range, and minimize homogenization of the gene pool or pools by anthropogenic activities. The recovery units in the *Recovery Plan*, with some exceptions described below, appear to reflect natural, biological differences in populations and to fall within the DPSs described in government policy (US Department of the Interior and US Department of Commerce 1996).

We emphasize, however, that the genetic evidence presented here is not necessarily concordant with or related to morphological, ecological, and behavioral differences observed in the tortoise populations. Genetic evidence is only one factor among many that should be considered in managing desert tortoises (Crandall et al. 2000; DeSalle and Amato 2004; Green 2005). No direct evidence suggests that the mtDNA and microsatellite markers reflect the observed phenotypic differences and local adaptations, although the assumption is that identified genetic markers may serve as surrogates for these and other character traits (Pearman 2001). Behavioral differences between populations can be genetically linked, as in the case of garter snake food habits (Arnold 1981) and morphological variability in turtles can be heritable (Myers et al. 2006).

In the absence of data linking genotypic markers with specific phenotypic characters or adaptations in desert tortoises, we are confined to delineating recovery units based on available information, such as the differences in mtDNA and microsatellite markers described here, as well as differences in vegetative communities, physical attributes of the habitat, climate (e.g., mean number of freezing days annually, mean annual precipitation, amounts of precipitation occurring in summer), choice and availability of forage plants, cover sites (burrows, dens), and denning behavior.

The direct translation of molecular data into management units is subjective. On one extreme, it is possible to define 2 recovery units, based on the arbitrary subdivision of assignment values. However, the STRUCTURE analysis indicated the presence of at least 6 genetically cohesive units. Although this evaluation was compromised by multidimensional IBD, when we reduced the effects of IBD, 4 additional genetic units were identified in the Western Mojave Recovery Unit: sample groups 1–2, 3–5, 8, and 6–7 plus 9–10 (Fig. 4). Ultimately, the designation of recovery units must synthesize all relevant factors to achieve effective management.

Our analyses indicate that the Western Mojave Recovery Unit should be divided into 3 regions (western, southern, and central) and 3 corresponding recovery units: Western Mojave, Central Mojave, and Southern Mojave (Table 8, Fig. 7). Although the analysis by using STRUCTURE discovered 4 genetic units within the Western Mojave, the segregation of 1 site (8) would not facilitate effective management. Our proposed recovery units are similar to the 3 Desert Wildlife Management Areas described in the *Recovery Plan* and are concordant with the western, southern, and central regions of the Mojave Desert described by botanists and climatologists (Rowlands et al. 1982; Rowlands 1995a, 1995b). The western, central, and southern Mojave regions differ primarily in the amounts of summer rainfall, number of freezing days, and mean January minima and mean July maxima temperatures, as well as in species richness (vegetation) and types and composition of plant species with different metabolic pathways, e.g., C_3, C_4, and Crassulacean acid metabolism (CAM). The redefined Western Mojave Recovery Unit (Fig. 7) receives precipitation primarily in winter and $< 10\%$ of rainfall occurs in summer (Rowlands 1995a; Table 8). The summer flora is very limited, and tortoises rely heavily on the succulent green forbs and herbaceous perennial plants available in late winter and spring (Jennings 1993, 2002; Oftedal 2002; Oftedal et al. 2002). The proposed Central Mojave Recovery Unit is the hottest and driest of the 3 regions and is low in botanical diversity (Rowlands, 1995a). Of the 3 regions, the proposed Southern Mojave Recovery Unit has more summer precipitation and a higher richness of C_4 and CAM plant species (Rowlands 1995a). Until ca. 100 years ago, the Southern Mojave Recovery Unit was physically separated from the proposed Central Mojave and Western Mojave recovery units by the Mojave River; human activities have since reduced or eliminated the flow along much of the river.

Climatic differences between all recovery units profoundly affect timing and availability of forage, as well as seasonal activities and very possibly depth of burrows and, thus, protection from freezing temperatures and the hot, dry summers. The existing eastern recovery units in the Mojave population have higher percentages of precipitation in the summer, thus supporting a more diverse and complex summer flora (Table 8; Rowlands 1995a, 1995b; Oftedal 2002). A winter flora is also available. Differences in the mean number of freezing days per annum contribute to seasonal activity periods and the types of winter hibernacula protecting the tortoises from freezing. The Northern and Eastern Colorado Desert recovery units are the warmest, with 1–16 freezing days/y compared with 29–127 freezing days/y in the Mojave. Northeastern recovery units are by far the coldest, possibly contributing to the well-developed dens and lengthy tunnels on Beaver Dam Slope (Woodbury and Hardy1948) that are rarely observed outside the Northeastern Mojave and Upper Virgin River recovery units.

Genetic assignments do not support a separation between the Eastern Mojave and Northern Colorado recovery units, possibly because we only had 4 sample groups from these regions. The close geographic proximities of the sample groups (Fig. 7) are unlikely to reflect the potential diversity occurring along a 250 km north-south axis. Until more data are gathered along the north-south axis, we do not recommend treating the 2 recovery units as one, because of major differences in climate, forage availability, and seasonal activities. These distinctions may be exactly the kind of ecological/adaptive differences worthy of conservation management, independent of the units delimited by neutral molecular variation (Crandall et al. 2000; Allendorf and Luikart 2007). Significantly, unlike the genetically restricted and legally inapplicable ESU, the legal application of DPS allows for and promotes such protection (US Department of the Interior and US Department of Commerce 1996).

The Northeastern Recovery Unit (group 11) and the Upper Virgin River Recovery Unit (group 15) showed the strongest differentiation (MDS plot, assignment test, and unique matriarchal lineage). They may be more genetically isolated than other areas. Both potentially show evidence of recent population reductions. Additional sampling of these regions is encouraged for evaluation of current management strategies. Unfortunately, under current legislation these and perhaps other demes cannot be protected solely on the basis of the degree of threat alone, as recently advocated by Green (2005).

Recovery Actions. — Populations that have become disjunct or mixed as a result of recent anthropogenic activities may be suitable for restorative actions (Crandall et al. 2000; Allendorf and Luikart 2007). One restorative action would be to remove deliberately or inadvertently

Table 8. Physical and biological attributes of proposed recovery units for the Mojave population.

Recovery unit	Mean annual precipitation (mm)	% Rainfall June–Sept	Mean no. freezing days annually	Mean July maximum temperature (°C)	Topography	Vegetation types
Western Mojave	90–150	3.1–9.9	33–84	35.4–37.4	Flats, valleys, alluvial fans, rolling hills, mountainous slopes	(1) Creosote Bush Scrub, (2) Mojave Saltbush-Allscale Scrub (endemic), (3) Indian Rice Grass Scrub-Steppe, (4) Hopsage scrub, (5) Cheesebush scrub (west Mojave type)
Central Mojave	109	18.3–20.7	57 +	39.1–42.9	Flats, valleys, alluvial fans, rolling hills, mountainous slopes, rock outcrops, badlands, sand dunes, lava flows	(1) Creosote Bush Scrub, (2) Big Galleta Scrub Steppe, (3) Hopsage Scrub, (4) Cheesebush scrub, (4) Desert Psammophytes
Southern Mojave	108	18.1–36.1	29–104	37.2–39.1	Flats, valleys, alluvial fans, rolling hills, mountainous slopes, rock outcrops, lava flows	(1) Creosote Bush Scrub, (2) Big Galleta Scrub Steppe, (3) Hopsage Scrub, (4) Cheesebush scrub, (4) Desert Psammophytes, (5) Blackbush Scrub
Eastern Mojave	112–208	27.5–37.7	34 +	34.8–36.1	Flats, valleys, alluvial fans, bajadas, rocky slopes	(1) Big Galleta-Scrub Steppe, (2) Succulent Scrub (*Yucca*, *Opuntia*), (3) Creosote Bush Scrub, (4) Cheesebush Scrub (eastern Mojave type), (5) Indian Rice Grass Scrub-Steppe
Northeastern Mojave	100–210	27.1–41.0	46–127	38.2–40.1	Flats, valleys, alluvial fans, rocky slopes, deeply cut washes	(1) Creosote Bush Scrub, (2) Big Galleta Scrub-Steppe, (3) Desert Needlegrass Scrub-Steppe, (4) Blackbush Scrub
Upper Virgin River	210	28.7	96 +	38.4	Rocks, caves, sandstone crevices, sand dunes	Transitional Vegetation: (1) Sagebrush Scrub, (2) Psammophytes, Great Basin (sand sage), (3) Blackbush Scrub
Northern Colorado	112–129	32.6–34.1	2–12	42.2–42.3	Flats, valleys, bajadas, rocky slopes, small washes	(1) Succulent Scrub (*Fouquieria, Opuntia*, *Yucca*), (2) Blue Palo Verde-Smoke Tree Woodland, (3) Creosote Bush Scrub (lava flows)
Eastern Colorado	96–100	32.3–34.4	1–16	40.5–42.2	Flats, valleys, alluvial fans, small washes, deeply dissected washes, rocky slopes	(1) Succulent Scrub (*Fouqueria, Opuntia, Yucca*), (2) Blue Palo Verde-Ironwood-Smoke Tree Woodland, (3) Creosote Bush Scrub (rocky slopes)

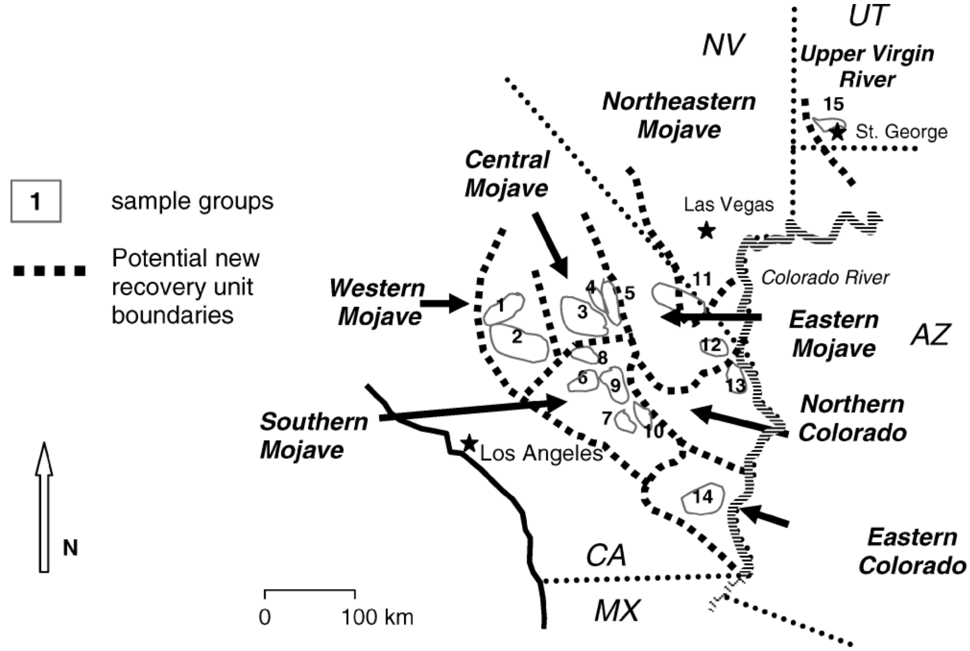

Figure 7. Sample groups of desert tortoises, *Gopherus agassizii*, shown with a new, preliminary alignment of recovery unit boundaries developed by using the mitochondrial deoxyribonucleic acid and microsatellite data presented in this study.

translocated tortoises from critical habitat. This strategy would be unreasonably difficult where populations are dense but may be a viable option where the area of interest and densities are limited, populations are declining, and most tortoises could be located and sampled. This strategy might be appropriate in the Upper Virgin River Recovery Unit and the Beaver Dam Slope Desert Wildlife Management Area (within the Northeastern Mojave Recovery Unit). Another restorative action would be to genetically test tortoises in the vicinity of frequently used recreation sites within national parks, research natural areas, and other protected areas: sites where visitors often release tortoises illegally, e.g., the Desert Tortoise Research Natural Area. The released tortoises from other populations could be identified and removed to a more appropriate place. In populations that have dropped below viable levels (e.g., Fremont-Kramer Desert Wildlife Management Area, Western Mojave Recovery Unit), informed and carefully planned augmentations or translocations could promote recovery, as has been done for a few other species (Allendorf and Luikart 2007). However, genetic planning is an essential part of such recovery efforts. Using tortoises within a well-defined recovery unit or local geographic area for headstarting or augmentation is far more desirable than translocating tortoises between recovery units. If local adaptations exist, then uninformed translocations of desert tortoises may do much more harm than good by introducing maladaptive genes into a locally adapted population.

Empirical studies need to be designed and tested to determine whether marker loci reflect specific adaptations with potential conservation value. For the Mojave population of the desert tortoise, the initial recovery units were defined on the basis of morphological, ecological, and behavioral differentiation, and the patterns of genetic variation parallel the earlier assessment in the *Recovery Plan*. Taken together, these 2 independent approaches strongly suggest the occurrence of local adaptation and evolutionary potential. Not only is it essential that this potential be conserved but also that underlying hypotheses be tested in the near future.

ACKNOWLEDGMENTS

We thank the Arizona Research Laboratories and staff at the Genomic Analysis and Technology Core for technical assistance, particularly M. Kaplan and H.-W. Herrmann. Samples from Arizona were contributed by C. Jones (University of Arizona) and D. Reidle (Arizona Game and Fish Department). At the Royal Ontario Museum, A. Lathrop, A. Ngo, and R. MacCulloch were helpful, and from California, A. Demmon was invaluable in processing samples. B.L. Burge and R.J. Turner provided historical data. K. Anderson, T. Bailey, R. Evans, R. Woodard, P. Woodman, P. Frank, B. Henen, and K. Nagy assisted by collecting samples. Valuable review comments were provided by D. Garrigan, K. Phillips, A. Russell, H.B. Shaffer, J.W. Sites, Jr., and J. Yee. A. Lathrop assisted with preparation of some figures and with GenBank submissions. Tissue samples were collected under federal and state permits to K.H. Berry (1994–2005), to K. Nagy for samples taken in the vicinity of Edwards Air Force Base, and to the late D.J. Morafka for samples along the southeastern boundary of Ft. Irwin. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US government. We are grateful for the financial support of the US Air Force, and Natural Sciences and Engineering Research Council (Discovery Grant 3148) to R.W. Murphy, and to the US Geological Survey, Bureau of Land Management, Department of the Army (National Training Center, Ft. Irwin, California), Marine Corps Air Ground Combat Center at Twentynine Palms, California and the California Department of Fish and Game to K.H. Berry.

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Received: 11 February 2006
Revised and Accepted: 31 August 2007

Ecology and Management of the Desert Tortoise (*Gopherus agassizii*) in California

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Abstract

The distribution and abundance of the desert tortoise (*Gopherus agassizii*) in California were determined from 137 surveys, each a square transect 1.6 km (1 mi) per side. Search was made for tortoises, burrows, scats, and other sign, and information was compiled for vegetation, soil type, and elevation. An index of relative density was combined with the broader habitat assessments to develop a map of the relative abundance of the tortoise in California. A distribution map is provided and a matrix delineates the range of environmental factors that affect the distribution and abundance of the tortoise in California. A review of the ecology of the species clarifies factors important to its survival. Land ownership patterns were identified and correlated with tortoise distribution to identify critical management areas. Information on the present and future status of the tortoise in California is discussed. Tortoise populations apparently are adversely affected by collection, roadkill, grazing, off-road vehicle use, and other human impact. Conservation efforts and management policies are reviewed and management needs listed.

A pronounced and steady decline in populations of the desert tortoise (*Gopherus agassizii*) in several parts of the southwestern United States has been noted for several years. Detrimental factors include encroachment by urbanization (Leach and Fisk 1969), collection by the pet trade and by individuals (G. R. Stewart, personal communication; Bury and Marlow 1973), highway mortality (Berry 1972, 1974*a*, 1975), overgrazing (Woodbury and Hardy 1948), maliciousness (Bury and Marlow 1973), and, most recently, off-road vehicle use (Bury et al. 1977; Luckenbach and Bury, in press). With increasing demands being made on the public lands of the California deserts, there was an apparent need for a better understanding of the status, distribution, habitat relations, and potential for management of the desert tortoise.

Objectives of this research were to: (1) assess the overall demographic status of the desert tortoise in California and, in particular, locate areas of high tortoise density; (2) study the natural history of desert tortoises and factors adversely affecting them; (3) evaluate tortoise habitat in terms of human disturbance; (4) determine ownership patterns of lands having tortoise populations; and (5) propose management programs to ensure the future of the tortoise and its desert home in California.

Materials and Methods

Procedures

To determine the abundance and status of the desert tortoise in California, I used a transect sampling procedure. I would drive or walk to a locality, stop and walk on a compass bearing for 1.6 km (1 mi), turn 90°, and continue to walk until a square transect 1.6 km on a side had been covered. I made 137 such transect surveys (a total of 880 km of walking observations) and made other casual surveys during related fieldwork. Surveys were conducted between June and October 1973, and in November 1974 and January 1975. Extensive observations were also made on habitat and other biota during the surveys. Between June and October 1973, I logged more than 14,000 km on the road and hiked 880 km. One helicopter and two fixed-wing flights supplemented the ground survey and provided additional data for mapping the extent of potential tortoise habitat.

Since the fieldwork was conducted during the late summer and early fall of 1973 and in the winter of 1974–75, peak above-ground activity was not encountered. Therefore, signs of tortoise rather than absolute tortoise numbers became important measures of tortoise abundance. Signs used were: (1) tortoise burrows, (2) scats, (3) shells, and (4) tracks. These measures of relative density were standardized by comparing the frequencies of these indicators from areas of known density with those from areas of unknown density.

The criteria used to determine the presence of desert tortoises were:

Burrow counts.—The relations between burrow numbers and tortoise numbers may vary greatly with geographic location (Auffenberg 1969) but is relatively consistent for some areas (see Auffenberg and Franz, this volume). Woodbury and Hardy (1948) report a ratio of 4:1 for summer burrows and winter dens. In California, a distinction between burrows and dens as defined by Woodbury and Hardy (1948) is difficult to make. A tortoise may use one burrow continuously for several weeks, then move and begin to use another (Marlow 1974). Alternatively, a tortoise may use several burrows within its home range. Further, some desert tortoises in California may spend the winter dormancy period in only a shallow burrow. I did not differentiate between summer burrows and winter dens—all were scored as burrows

In making burrow counts, I noted the size and shape of the burrow as well as activity indicators such as plastron-slide marks, the amount of debris at the mouth of the burrow, lack of spider webs or the crescent shape of existent webbing, and tracks. I used these criteria to determine whether a burrow was occupied and to estimate the approximate size of the animal using it. A flashlight or reflective mirror was often used to light the interior of burrows. Probing with a meter stick sometimes caused tortoises to stir and, occasionally, pounding on the ground at the entrance caused a tortoise to emerge. Because signs of burrow use are often lacking during the fall and winter, it is almost impossible to determine whether a burrow is occupied unless the animal is in sight. Locating burrows is crucial in the censusing process and careful, concentrated search not only of open ground but also around bushes is necessary to find all the burrows along a transect.

Tortoise burrows are distinctly crescent-shaped and slant downward at a slight angle. If the burrow entrance was small and crescent-shaped, but suddenly tapered to a rounded hole, it was assumed to be the burrow of a kangaroo rat (*Dipodomys* sp.). Ground squirrels (*Spermophilus* and *Ammospermophilus*) also construct round holes. Burrows constructed by juvenile tortoises are small and may resemble rodent or lizard burrows. Illumination of the burrow interior usually is needed for accurate identification of the animal that built it. The size of a tortoise burrow is related to the size of the animal using it. For example, an adult male with a carapace length of 25.1 cm (examined near Daggett, San Bernardino County, on 23 August 1973) occupied a burrow 38.5 cm wide and 17.5 cm high.

Scats.—The presence of scats confirms that a tortoise once used an area, and the size of the scat is an indicator of the size of the tortoise. A medium-sized female (129 mm carapace length) deposited scats that averaged 16.3 mm long (N=13). Tortoise scats are distinctive (Fig. 1), and with practice can be distinguished from the fecal material of any other desert vertebrate. They are cylindrical, often tapered to a point at one end, and composed largely of vegetable matter; some contain large amounts of sand and grit or consist entirely of sand. Recently deposited scats have a shiny, blackish coating; with exposure, this coating wears off and the scat disintegrates rapidly. Scats deposited in early spring disintegrate readily because they are composed of flowering stalks and other succulent portions of annuals. Summer food consists largely of the dry portions of annuals, especially grasses, and scats containing these persist for longer intervals. Predator scats were also examined to determine presence of tortoise remains.

Tortoise shells.—The presence of tortoise shells also indicates that tortoises live (or formerly lived) in an area. However, since shells may be transported by carnivores and humans, their presence in a particular locality does not necessarily mean that the tortoise succumbed at that site.

The deterioration of the shell gives some indication of time since the animal's death (Berry 1974*a*, 1975). The horny scutes may adhere tightly to the bony skeleton from 6 months to 1 year; over a period of 1-2 years, they gradually dry, lighten in color, and peel. The underlying bony structure of the shell then begins to disintegrate—a process that may take from 2 to 5 years.

Fig. 1. Examples of desert tortoise scats from a series collected near Hinkley, San Bernardino County, California. In the right column, the top three consist of large amounts of sand and gravel, and the bottom two are relatively old scats that show weathering (from Luckenbach 1976).

Fig. 2. Desert tortoise tracks made in aeolian sand. Tail drag between tracks probably indicates a male (from Luckenbach 1976).

Tortoise tracks—The use of tortoise tracks in estimating population size is of limited value. Tracks may be visible only in areas of sand or soft soil and may reflect only periods of above-ground activity. Careful tracking of individual tortoises may yield data on home range size, burrow usage, feeding habits, and reproductive state. Copulating animals may often leave a small, round depression as well as signs of recent urination. If tracks lead to a certain plant, close examination may reveal whether the plant has been eaten.

Figure 2 shows tracks made in aeolian sand near Hinkley, San Bernardino County. Note that the main track is left by the hind foot pad while the forelimbs left only a small depression; note also the tail drag, indicative of males.

Estimation of Population Density

Population density (individuals per unit area) is measured in many ways (for reviews see Southwood 1966; Lamotte and Bourliere 1969; and Seber 1973). The ideal is to measure absolute density (the total number of individuals within a defined area or community) by: (a) counting total population, (b) harvesting, and (c) estimating from survey techniques such as mark-recapture indices or intensive quadrat sampling. The method selected depends on the nature of the animal species and the length of time that can be devoted to the study.

Because of time constraints and the large size of the census area, I measured the relative density of tortoise populations. Determining relative density depends on collecting or measuring samples that represent a relatively constant but unknown relation to the population size. Although such an estimate is not a reliable measure of absolute density, it is a useful index for comparing populations.

Population estimates for the Desert Tortoise Reserve, Kern County, California, are given by Marlow (1974 and personal communication), and I determined the density of tortoises for an area north of Hinkley, San Bernardino County. Transect samples from these two areas yielded a baseline of known absolute density with which to

Table 1. *Comparison of survey data from the Desert Tortoise Reserve and Hinkley Site and from 137 transect surveys. N = number of transects assigned to a density category. Transects are listed in the Appendix. Values are $\bar{x} \pm$ S.D. (Range).*

		No. of tortoises		No. of burrows		Scats	Relative density [a]
	N	Adult	Juv.	Active	Inactive		(km²)
Desert Tortoise Reserve	5	22.8±13.0 (8-43)	1.4±1.9 (0-4)	44.8±9.2 (36-60)	41.2±4.8 (36-48)	19.6±3.0 (16-24)	358
Hinkley	5	14.4 ± 3.4 (9-18)	0.8±0.8 (0-2)	26.0±7.6 (16-36)	18.8±4.4 (12-24)	22.8±9.6 (12-36)	217
High density	33	4.4 ± 3.0 (0-10)	0.8±1.0 (0-3)	30.7±7.8 (18-47)	28.3±6.0 (17-37)	11.9±7.7 (0-32)	157
Medium density	69	3.0 ± 2.8 (0-11)	0.7±1.0 (0-4)	13.2±5.6 (3-29)	8.8±5.2 (0-21)	6.0±5.1 (0-20)	79
Low density	35	1.0 ± 1.2 (0-4)	0.2±0.4 (0-1)	4.6±4.9 (0-19)	2.8±3.4 (0-11)	1.1±2.2 (0-7)	27

[a] Relative density is determined by the formula:
No. Ad. + No. Juv. + Active Burrows ÷ 2 = X (No. per 13 ha); X ÷ 0.13 = No. per km².

compare transect surveys (Table 1). The number of tortoises encountered during each transect was extrapolated to density estimates per square kilometer. The ratio of active burrows to tortoises on the Desert Tortoise Reserve is about 2:1 (R. W. Marlow, personal communication). Assuming a ratio of 2 burrows per tortoise, I estimated tortoise numbers by burrow counts and used this ratio throughout my census.

The survey areas were transects 6.4 km long and covered a width of 20 m (10 m on each side of the path). Burrows were often difficult to detect beyond this limit since they were easily obscured by bushes. The total area covered on each line transect (20 m x 6.4 km) was 13 ha. I extrapolated the counts from each survey to densities per square kilometer. These estimates should be recognized as only approximations of population size.

Data from ground and air surveys (1973 and 1974-75) were combined to develop density patterns over the California desert. Distinctions are made for high, medium, and low population levels. High population densities are considered to be more than 155 tortoises/km², medium to be 40-155/km², and low to be less than 40/km². Density patterns are based on a combination of factors: evidence of tortoise presence from surveys, habitat condition, and degree of habitat disturbance.

Extent of Survey

The survey encompassed the Mojave Desert and Colorado Desert of California. The principal geographic and land features of this region are provided in Fig. 3; my field survey sites are shown in Fig. 4.

Coverage of the California deserts varied. In the northwest Mojave Desert, extensive surveys were made of areas along State Highways 58, 14, and 395 and along dirt roads in the El Paso and Rainbow Basin Mountains and in the Harper and Water Valleys. Limited reconnaissance was made along the eastern flanks of the Sierra Nevada to determine elevational limits of tortoises in the foothills. Searles Valley was poorly surveyed, and Panamint Valley was not surveyed at all. Because of the large number of privately owned land parcels and housing developments, the area of Antelope Valley and Victorville was surveyed only briefly. In the central Mojave Desert, a careful survey was made in the area north of Hinkley and in the area southeast of Barstow—the Stoddard Valley; the Ord, Rodman, and Newberry Mountains; and the eastern end of Lucerne Valley. The alluvial flanks of both the Cady and Bristol Mountains were also thoroughly checked. A reconnaissance was done in the Yucca-Twentynine

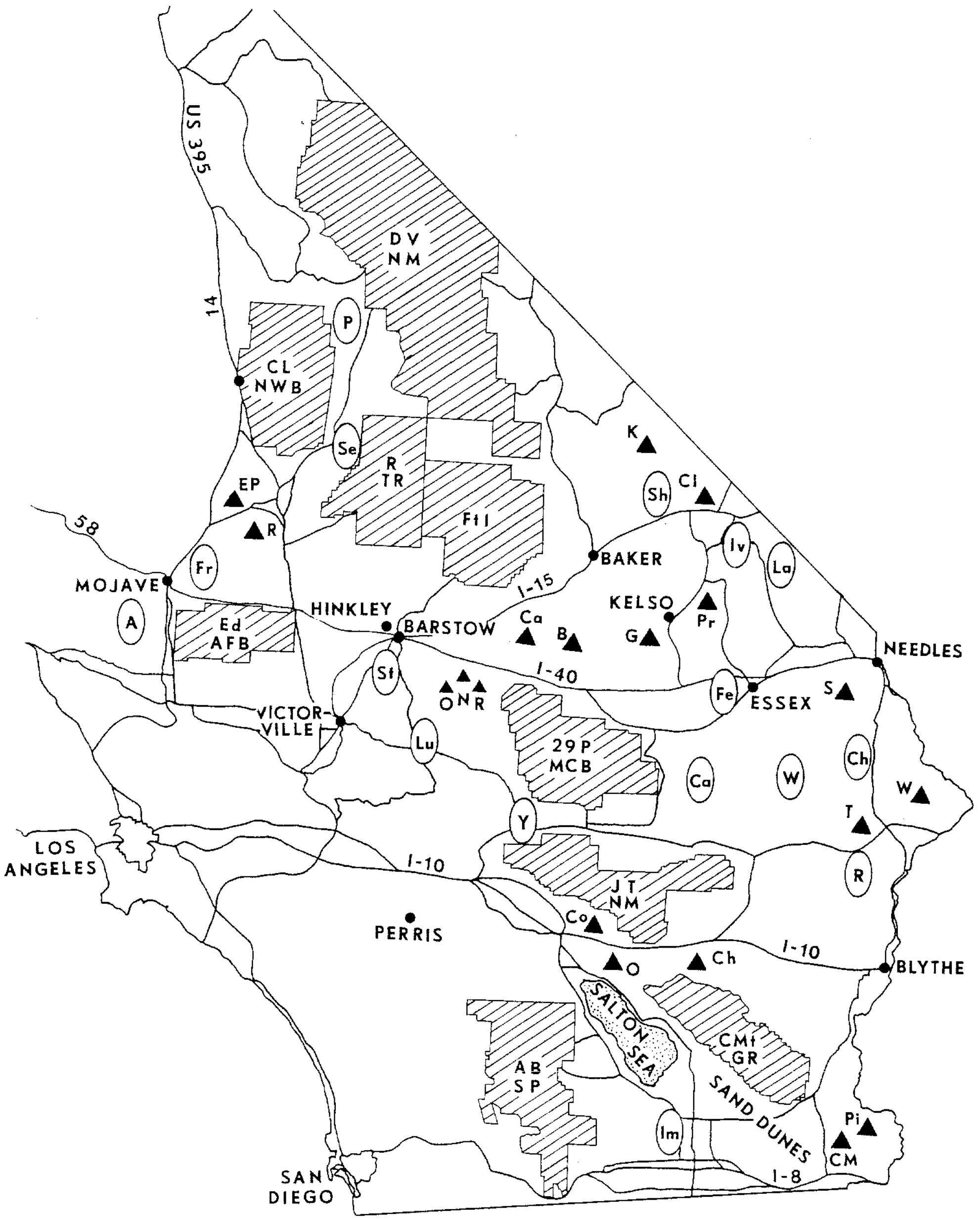

Fig. 3. Major geographic features of the California Desert that are mentioned in the text.

Abbreviations of military and park lands are: Death Valley National Monument; Joshua Tree National Monument; Anza Borrego State Park; China Lake Naval Weapons Base; Randsburg Test Range; Fort Irwin; Edwards Air Force Base; Twentynine Palms Marine Corps Base; Chocolate Mountains Gunnery Range.

Major mountain ranges are indicated by triangles: B—Bristol; Ca—Cady; Ch—Chuckwalla; Cl—Clark; Co—Cottonwood; CM—Cargo Muchacho; EP—El Paso; G—Granite; K—Kingston; O—Orocopia; Pi—Picacho; Pr—Providence; R—Rand; S—Sacramento; T—Turtle; W—Whipple.

Major valleys are enclosed in ellipses: A—Antelope; Ca—Cadiz; Ch—Chemehuevi; Fe—Fenner; Fr—Fremont; Im—Imperial; Iv—Ivanpah; La—Lanfair; Lu—Lucerne; P—Panamint; R—Rice; Se—Searles; Sh—Shadow; St—Stoddard; W—Ward; Y—Yucca.

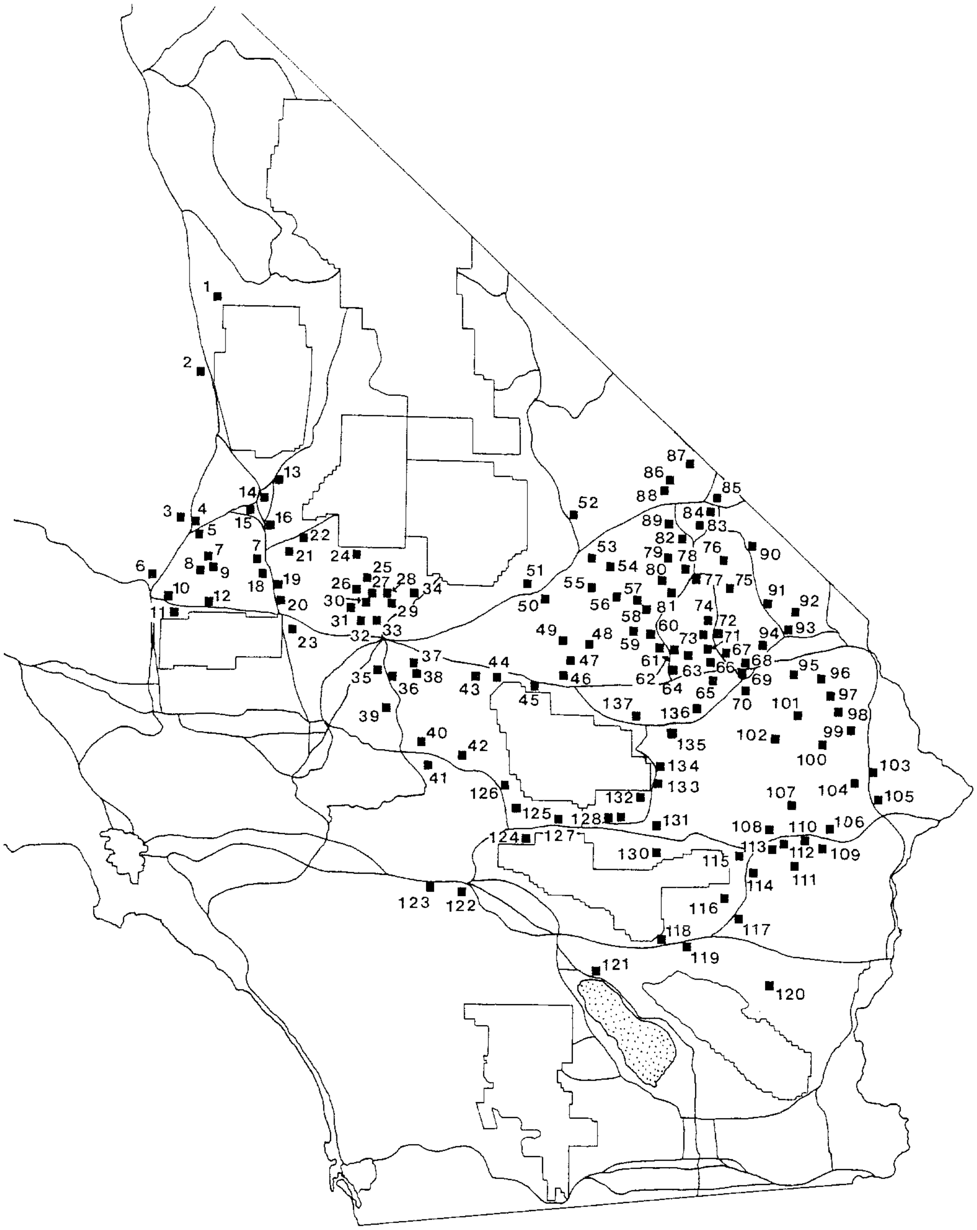

Fig. 4. Field survey sites in California. Numbers refer to transects listed in the Appendix.

Palms area and in the Mojave Valley. Joshua Tree National Monument was excluded from this study because captives have been repeatedly introduced, and animals there are already protected. In the eastern Mojave Desert, the area south of Interstate 15 (in particular, the Cima-Providence Mountains-Essex region) was surveyed intensively. The valley north of Baker, the upper half of Shadow Valley, and Mesquite Valley were surveyed to a lesser extent. The area north of the Avawatz and Shadow Mountains and the Kingston Range was visited briefly. South of the Providence Mountains, field surveys were concentrated in the Fenner, Ward, and Chemehuevi Valleys. The area adjacent to the Colorado River, south of Needles, was not surveyed. In the Colorado Desert, the survey was confined to areas east of the Salton-Imperial Valley trough. Palen Valley was the region most thoroughly surveyed. Most of the transects and field reconnaissance work in this area was conducted during August and September 1973, when extreme heat made fieldwork difficult. The Colorado-Sonoran portion of the California deserts thus received only cursory coverage, and the Cargo Muchacho and Picacho Mountains were not surveyed.

China Lake Naval Ordnance Test Station, Fort Irwin, Edwards Air Force Base, Twentynine Palms Marine Corps Training Center, and the Chocolate Mountains bombing range were excluded from this study for logistic reasons.

Land ownership patterns of the desert lands surveyed were also determined. Basic information was obtained from the Bureau of Land Management's (BLM) Resource and Recreation maps (Nos. 8-11, 16; scale 1:250,000; available from the Bureau of Land Management, 2800 Cottage Way, Rm. E-2841, Sacramento, California 95825) and from county records.

Distribution of *Gopherus agassizii* in California

During the surveys, vegetation, soil type, and elevation were recorded. Tortoise presence was then correlated with these environmental factors to provide an environmental matrix for the desert tortoise (Fig. 5).

Precipitation was estimated from elevation and the nature of the plant community. Estimation of the annual bloom potential was subjective, although the criteria were based in part on the amount of remnant annual growth plus elevation and soil type. Perennial diversity was derived by comparison of the number of different perennial species present in survey areas. Vegetation, soil, and elevation in relation to tortoise distribution and abundance are discussed in the following sections.

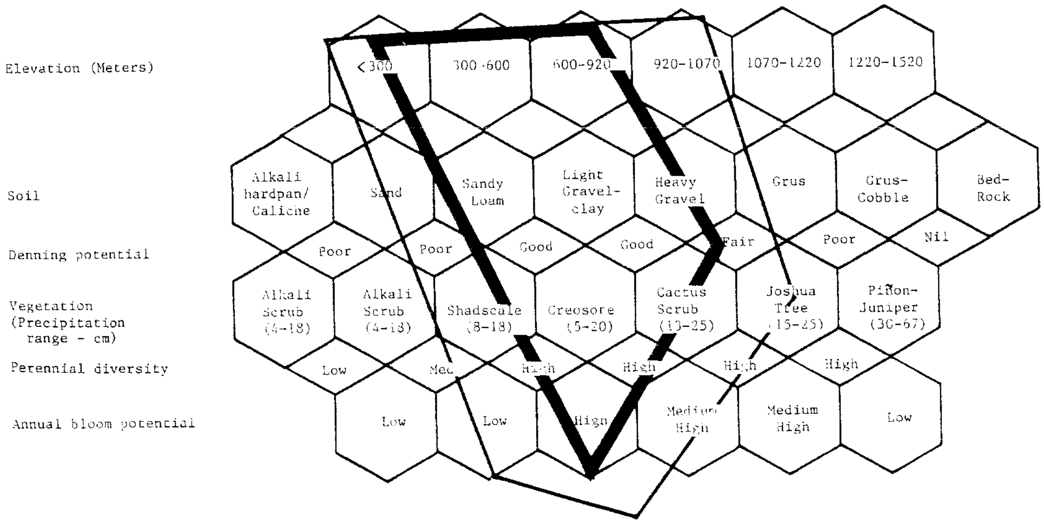

Fig. 5. Environmental matrix for the Desert tortoise in California. Thick line indicates the preferred range, thin line the estimated potential range.

Vegetation

Discussion of the distribution of tortoises in California in relation to vegetation necessitates assessment of the vegetational communities of the California desert. Recent reviews of the desert vegetation of California can be found in Johnson (1976) and Barbour and Major (1977). Following the community structure of Munz and Keck (1959), four scrub communities (alkali, creosote, shadscale, and sagebrush) and two woodland communities (Joshua tree and pinon-juniper) are recognized in the California deserts.

Creosote bush (*Larrea tridentata*) is the dominant plant and forms the major community on well-drained sandy flats, bajadas, and upland alluvial slopes throughout both the Mojave and Colorado-Sonoran Deserts. Commonly, *Larrea* forms associations with other perennials. Beatley (1969) recognized six *Larrea*-dominated associations in southern Nevada. I have discerned seven such associations in the Providence Mountains region in the eastern Mojave Desert of California. The creosote-burroweed association (*Larrea tridentata-Ambrosia dumosa*) is the most characteristic and constitutes as much as 70% of the Mojave Desert (Shreve 1942).

Low-lying areas of bolsons and valleys characterized by saline soils display alkali scrub communities. The important components consist of halophytic species such as saltbush (*Atriplex* sp.) and succulent chenopods of the genera *Allenrolfea*, *Salicornia*, *Suaeda*, and *Sarcobatus*.

At slightly higher (1,200-1,800 m) and sometimes at drier sites than those where creosote scrub predominate, vegetation usually consists of low shrubs broadly classified as shadscale scrub. In the northern Mojave, where contact with the Great Basin Desert occurs, shadscale scrub composed chiefly of shadscale (*Atriplex confertifolia*) and sagebrush (*Artemisia spinescens*) is distinct from creosote scrub and sagebrush scrub. Over most of the Mojave Desert, shadscale scrub is dominated by blackbrush (*Coleogyne ramosissima*) in conjunction with various species of yucca (*Yucca* spp.), Mormon tea (*Ephedra* spp.), and cholla (*Opuntia* spp.).

Sagebrush scrub is the typical Great Basin association and is dominated by the Great Basin sage (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*). It is common at higher and colder sites than are typical of the Mojave Desert. Sagebrush scrub is largely restricted to the eastern highland areas in the California Desert.

The most conspicuous plant of the Mojave Desert is the endemic Joshua tree (*Yucca brevifolia*), which forms a characteristic woodland on well-drained soils in areas of moderate rainfall (more than 24 cm per year). Joshua trees form overstories with many scrub associations; at higher elevations, they grade into juniper (*Juniperus californica* or *J. osteosperma*) or pinon woodland (*Pinus monophylla*).

Vegetational patterns are more diverse than can be described in a single community framework. Ecotones, gradations, and combinations of communities are common. Creosote can form associations with any one of the other scrub or woodland communities. Other communities may be limited in area but locally important. Although not recognized as a separate community, cactus scrub is important in both the Mojave and Colorado-Sonoran Deserts. In the Mojave, it most commonly consists of a jumping cholla (*Opuntia bigelovii*) and burroweed (*Ambrosia dumosa*) association. It is present in the Sacramento and Woods Mountains, and in Ward Valley, San Bernardino County. In the Colorado-Sonoran Desert, cholla (*Opuntia*), cacti (*Echinocactus*, *Echinocereus*), and other stem succulents comprise the cactus scrub.

Margins of arroyos often support distinctive plant associations. I discerned at least six wash associations in the region of the Providence Mountains. In the Colorado-Sonoran Desert, wash vegetation often forms dense thickets that can be considered a wash woodland community.

Thorne (1976) lists four other groups as separate recognizable vegetative communities: desert rock plants, desert dune sand, semisucculent scrub, and desert microphyll woodland.

In the California deserts, *G. agassizii* mostly frequents four communities: creosote scrub, cactus scrub, shadscale scrub, and Joshua tree woodland (Fig. 5). Sometimes tortoises occur in alkali scrub.

Soils, Topography, and Flora

Soil type is an important limiting factor for tortoises. Probably no type is preferred, but the soil must be friable enough for the digging of burrows and firm enough so that burrows will not collapse. In the areas of high tortoise population density, soil type varies from gravelly flats in Stoddard Valley to sandy soil with some clay content in the Fremont Valley, and to fine, windblown sand and stabilized dunes near Hinkley and in the Pinto Basin of Joshua Tree National

Monument. Tortoises, however, are absent or scarce in most other sandy areas such as the Algodones and Kelso Dunes.

Creosote scrub occurs on a range of soils from cobble or desert pavement to sand. However, it is often excluded from fine-textured basin soils of high salinity and low oxygen content (Lunt et al. 1973). These soil characteristics negatively affect the growth of annual vegetation and thus ultimately lower the carrying capacity of alkali scrub for tortoise populations.

Desert tortoises may be found in rocky areas. In the Mojave Desert, cactus scrub is often best developed on rocky substrate such as dissected rocky benches; tortoises frequent such areas. In the Colorado Sonoran Desert, cactus scrub seems to occur on south-facing slopes or fine-grained soils. Tortoises are less common here than in adjacent creosote scrub or wash woodland areas. The upper parts of bajadas and alluvial fans are generally too rocky for burrow construction.

Pinyon-juniper woodland is found in the western Mojave Desert above 1,200 m on the flanks of the Sierra Nevada and San Bernardino Mountains or on isolated ranges. Below this rim, Joshua tree woodland occurs in areas of moderate rainfall or intermediate elevation (760-1,200 m). Soils of this Joshua tree woodland vary from granitic gravels along the Sierra Nevada piedmont to sandy soils in the Antelope, Yucca, Fremont, and Harper Valleys. Below 1,000 m on well-drained alluvial soils, the vegetation is dominated by creosote scrub. The spring aspect is one of green shrubs and showy spring flowers; the late summer aspect is of dull-colored shrubs and scattered dry bunchgrass (*Oryzopsis hymenoides, Hilaria rigida, Schismus barbatus, Stipa speciosa*). Poorly drained soils often have caliche layers and are characterized by the presence of shadscale scrub. Playa and alkali flats display elements of alkali scrub or are devoid of vegetation.

In the western Mojave Desert, the greatest density of free-living desert tortoises found thus far occurs in creosote scrub in the Fremont Valley (Fig. 6), an area of relatively uniform creosote habitat with light gravel to sandy soil. Tortoises are found also in Joshua tree woodland, but the shrub story in most of the western Mojave is a dense

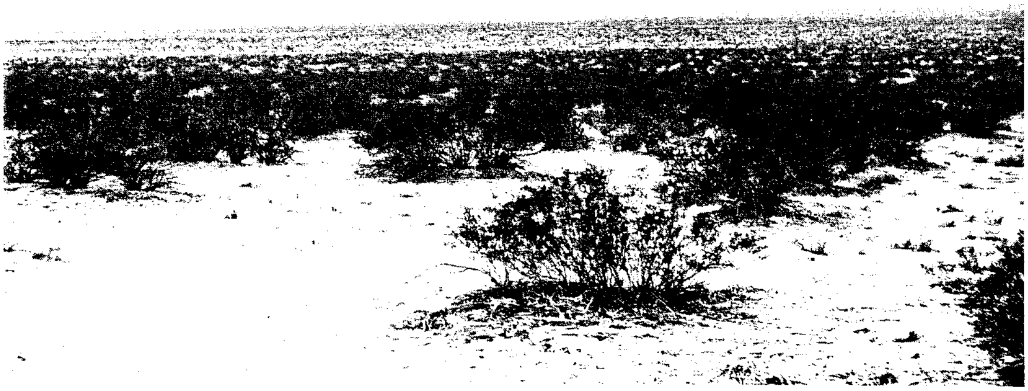

Fig. 6. Area of high tortoise population density in western Mojave Desert. Creosote-burroweed association in the Desert Tortoise Reserve, Kern County, California.

Fig. 7. High tortoise density area north of Hinkley, San Bernardino County, California. Joshua tree and creosote-burroweed associations. Soils here are sandy.

creosote association. Tortoises are also found in moderate numbers in areas of alkali scrub habitat. Around Koehn Dry Lake, tortoises were found in an area of stabilized sand hummocks with mesquite (*Prosopis juliflora*) and saltbush (*Atriplex* spp.). In the area south and west of Fremont Peak and towards Kramer Junction and near Hinkley (Fig. 7), an area with extensive stands of saltbush (*Atriplex confertifolia* and *A. polycarpa*) in mostly sandy soils, tortoises are common but less so than on adjacent creosote shrub habitats.

Topography of the eastern Mojave Desert is varied, with elevations above 2,100 m in the Providence Mountains and Kingston Range, and more than 2,400 m in the Clark Mountains. Physiographically, this area is an extension of the Basin and Range Province; the basins are seldom lower than 760 m, and the area is typified by great relief. Several vegetational communities may be encountered within short distances. Like the western Mojave, most of the eastern Mojave Desert is considerably higher than the Colorado Desert.

Climatic diversity is high in the eastern Mojave Desert, and much of the area adjacent to the Colorado River often experiences late summer thunderstorm activity. These storms are generated by easterly airflow from the south Atlantic Ocean, which crosses the Gulf of Mexico and continues across Texas, New Mexico, and Arizona. Partly dissipated cells of low air pressure linger over the Colorado River and are "revitalized" by moisture-laden convective air. Periodic strengthening of easterly airflow patterns causes these cells to move westward, and convectively- and orographically-induced precipitation results. Such thunderstorms may be intense, though brief and highly localized; flash flooding frequently accompanies them. Some eastern Mojave areas receive two peaks of annual precipitation—the normal winter peak and variable summer rains. This bimodality of rainfall resembles that of the Arizona-Sonoran Desert. Low-lying areas immediately west of the Colorado River from about Needles south to the vicinity of Blythe can be considered as a portion of the Arizona-Sonoran Desert. This bimodal rainfall pattern has resulted in diverse vegetational communities. Annual plants respond with two flowering peaks, one in the spring and the other in the fall.

Biotically, the Providence-New York-Granite Mountains represent a meeting of four deserts of the Southwest: the Great Basin, Mojave, Colorado-Sonoran, and Arizona-Sonoran Deserts. This confluence is reflected by the great diversity of the regional flora and fauna. Piñon-juniper woodland with Great Basin sage (*Artemisia tridentata*) are found between 1,070 and 2,100 m. Two piñon pines (*Pinus edulis* and *P. monophylla*) occur together in the Ivanpah Range. At mid-elevations, elements of the Arizona-Sonoran Desert finger into the Providence Mountains and other ranges bordering the Colorado River. The northernmost limit of the Colorado-Sonoran Desert is found here. Ocotillo (*Fouquieria splendens*) and ironwood (*Olneya tesota*) are found in washes at lower elevations. Typical Mojavean vegetation is dominant on level areas at lower elevations. The finest stands of Joshua trees in the Southwest occur in the Lanfair Valley and Cima Dome area; these trees are the short-leafed variety (*Yucca brevifolia* var. *Jaegeriana*).

Rocky areas at elevations from 900 to 1,200 m are dominated by succulent vegetation. Chollas in Woods Mountains and in the upper Ward Valley (Camino Valley) develop into large gardens. Barrel cactus (*Echinocactus acanthodes*) is limited to an altitudinal belt of 900-1,500 m. Mojave yucca (*Yucca schidigera*) is also distinctive in this belt, although it also extends to lower elevations. Below 850 m, the predominant vegetation is creosote scrub. Along the south flank of the Providence Mountains, creosote scrub yields to a mixed buckwheat scrub community, and washes are numerous. Alkali scrub is typical around the numerous dry lake beds of the area.

The large Dumont and Kelso dune systems and a minor crescent system south of Soda Lake bed are adjacent to Providence Mountains. Other areas of aeolian sand deposition include southern Cadiz Valley, the Dale area, lower Ward Valley, and the Rice Valley.

Desert tortoises in the eastern Mojave Desert occur predominantly in creosote scrub, cactus scrub, and Joshua tree woodland and, sparsely, in shadscale scrub. On the lower slopes of bajadas, tortoises are commonly found in wash habitats.

The Colorado-Sonoran Desert is warmer than the Mojave and has basins lower in elevation than those of the Mojave. Yearly precipitation here is also bimodal. Dominant plant cover consists of the *Larrea-Ambrosia* association in conjunction with brittlebush (*Encelia farinosa*) and ocotillo. Bushes are widely spaced, and the aspect is desolate. Creosote scrub is best developed on coarse, well-drained soils with low salinity, whereas alkali shrub occurs in heavier soils and in salt-laden areas. Development of arborescent species is pronounced in the Colorado-Sonoran Desert, resulting in varied wash associations, and detrital fan aprons are incised by numerous sandy washes. The bases of the Cottonwood, Eagle, and Chocolate Mountains are etched by dendritic arroyos, where the vegetative cover is primarily an arborescent wash woodland. Smoke tree (*Dalea spinosa*), Palo verde (*Cercidium floridum*), ironwood, and desert willow (*Chilopsis linearis*) are common in these washes.

Between Yuma, Arizona, and the Imperial Valley of California is a north-south series of large sand dunes — the Algodones Dunes. Creosote bushes and the shrubby buckwheat (*Eriogonum deserticola*) attain large size on the lower slopes of these dunes. East and north of the Salton Sea are isolated oases of fan palm (*Washingtonia filifera*). Similarly, isolated stands of saguaros (*Cereus giganteus*) occur on the eastern end of the Little Chuckwalla and Whipple Mountains.

Tortoises are mostly uncommon in the Colorado-Sonoran Desert. Where they occur, vegetation consists of creosote scrub or wash woodland associations. In the Palen and Chuckwalla Valleys and on the Palo Verde Mesa, tortoises occur in creosote scrub and occasionally in cactus scrub.

On the western and eastern flanks of the Chocolate and Cottonwood Mountains, tortoises are found in association with wash habitats. No tortoises were found in the sandy areas of the Algodones Dunes or in the dense creosote scrub of the East Mesa (east of the Imperial Valley). Recently, Dimmitt (1977) found few tortoises in the Algodones region but located moderately dense populations (active burrows 54-93/km^2) in washes and bajadas of the Cottonwood Mountains and Chuckwalla Bench (northeast of the Salton Sea).

The abundance and diversity of perennial vegetation apparently indicate the overall potential of a habitat to support tortoise populations. Diverse and lush shrub growth is only possible where rainfall is sufficient. Rainfall also governs the potential for blooms of the ephemeral plants (annuals and some herbaceous perennials) which are the prime forage for tortoises. Biomass of ephemerals is apparently critical as the food supply for California tortoises.

Elevation

Although chiefly an inhabitant of the Lower Sonoran Life Zone, the desert tortoise occasionally ranges into the Upper Sonoran. Tortoises are known from elevations ranging from below sea level in Death Valley to 2,256 m in the Clark Mountains (Johnson et al. 1948). The Clark Mountain record was a shell that may have been carried to this altitude. Recently, two live individuals were found in Wildrose Canyon, Death Valley National Monument, at elevations of 1,280 and 2,225 m (P. Sanchez, personal communication). I have found tortoise burrows at 1,463 m in Cedar Canyon in the Providence Mountains and at 1,158 m near the Woods Mountains. Tortoises seldom range above 915 m along the flank of the Sierra Nevada or San Bernardino Mountains and only infrequently occur above 1,000 m throughout the western Mojave Desert.

Tortoise burrows were found in the Kelso Valley, Kern County (Kelso Valley is only a few kilometers from the Kern River drainage). Given suitable environmental conditions, a tortoise could follow the dry bed of the Kern River into the San Joaquin Valley. Such movement may have been responsible for its presence during the Pleistocene at McKittrick in the San Joaquin Valley (Miller 1932).

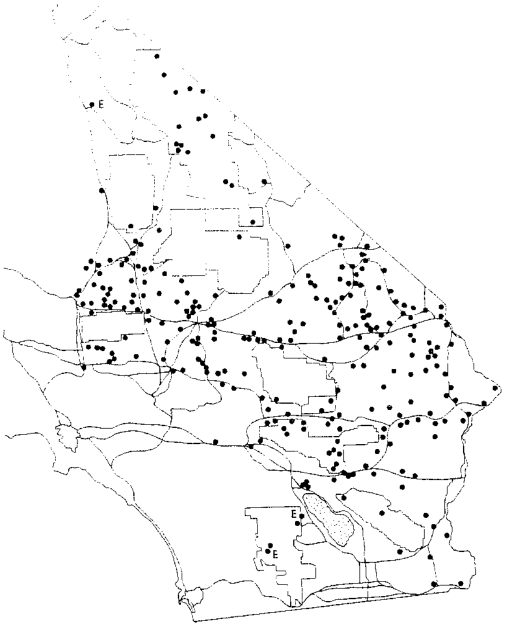

Fig. 8. Distribution of *Gopherus agassizii* in California. E = Extralimital localities.

Distributional Limits

The distribution of *G. agassizii* in California shown in Fig. 8 is based on animals encountered in my field surveys and on museum records. The large number of pets released in California complicated the determination of the natural range. For example, the tortoise pictured by Carr (1952) from Perris, Riverside County, was probably a pet (J. St. Amant, personal communication).

Numerous tortoise breeders defend their practice on the basis that they release a portion of the young that are hatched. The Antelope Valley is near the Los Angeles metropolitan area and has long been a release site for liberated pets. Some 300 were released in Saddlebag Butte State Park in the Antelope Valley in 1975–76. Between 1971 and 1972, 65 tortoises were released in the Vallecito Mountains within Anza Borrego Desert State Park, which is an area outside the natural range of *G. agassizii*. Some reproduction of these animals has been reported (M. Getty, personal communication).

Results of Field Survey

Western Mojave Desert

The highest known population density of desert tortoises in California is in the Fremont Valley (Table 1). Tortoise population densities determined by R. W. Marlow (personal communication) on plots adjacent to the Desert Tortoise Reserve north of California City ranged from 347 to 540/km². This is an area of diverse perennial scrublands, relatively high rainfall (15 cm/year or more), and excellent ephemeral blooms. Soils are broadly red deserts, predominately sandy loams. Similar population densities appear to continue in a belt from the Fremont Valley and just north of State Highway 58 along the southern flanks of the Rand Mountains to the southern portion of Fremont Peak, then numbers decrease north of Harper Lake and south of the Rainbow Basin–Opal Mountain area (Fig. 9). Vegetation in this area is predominately shrubs and scattered stands of Joshua trees.

Areas of wind-blown sand are found east of the town of Mojave, to the northeast of Harper Lake, and at the east end of Koehn Lake. Although subject to deflation, these sand areas support relatively high tortoise populations. Some tortoises occur in the Pinto Basin (Joshua Tree National Monument) and Dale Dry Lake in the central Mojave Desert. Elsewhere in the Mojave and Colorado Deserts, sandy areas seem to lack viable tortoise populations.

The second highest known density of tortoise populations is in an area north of Hinkley. This area is largely wind-blown and stabilized sand on top of tertiary lava flows, with scattered Joshua trees and numerous washes. Estimates made from mark-recapture data compiled by D. and N. Shade (of Twentynine Palms) and from my surveys indicate a population of 116-193/km². The Barstow Unified School District's Desert Research Station (5 km north of Hinkley) has a known population of about 77/km² on a more rocky substrate (L. Hunter, personal communication).

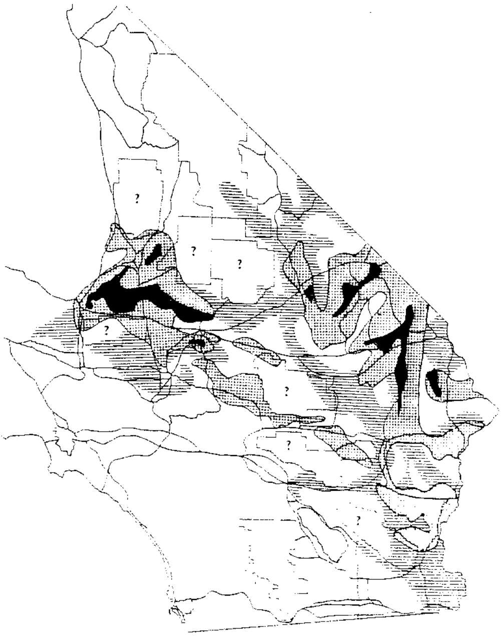

Fig. 9. Relative densities of *Gopherus agassizii* in California. Dark areas indicate high densities; cross-hatching, medium densities; horizontal lines, low densities; and question marks, unknown areas (mostly on military bases). See text for explanation.

In the past, high densities of *G. agassizii* undoubtedly extended from the Fremont Valley into the Antelope Valley. These valleys are similar in that they receive large amounts of winter rainfall, have diverse perennial vegetation (Antelope Valley is mostly Joshua tree woodland), and are noted for exceptional spring ephemeral blooms. Homesteading, subdivisions, and other human pressures have greatly reduced the tortoise population in the Antelope Valley. Although populations survive in small parcels of habitat, they are apparently declining. If proposals for a giant jet airport in the Antelope Valley materialize, the impact on the remaining desert environment in this area could be catastrophic. East of the town of Mojave, improvement of Highway 58 into an interstate highway necessitated a relocation of some tortoises, but the project had only limited success. The relocation effort demonstrated some homing abilities in desert tortoises (Berry 1974*a,b*).

Other known high-density populations occur west of Hinkley Valley, in the Stoddard and Upper Lucerne valleys, and in the vicinity of Fry Mountain. Isolated populations occur near Helendale, Victorville, and Mojave Valley; all are areas rapidly being developed for housing tracts. Natural habitat is poor in the Cady and Bristol Mountains. Resident populations have been all but eliminated from Lucerne Valley and the area of Yucca Valley and Twentynine Palms, Victorville, and portions of the Antelope Valley.

Eastern Mojave Desert

Tortoise habitat in the eastern Mojave Desert often was found in areas of extensive desert pavement with washes and a vegetational aspect of widely scattered cacti and creosote shrubs on the flats with smoke trees and mesquites in the washes.

Tortoise population densities were high in the Ivanpah Valley, on the periphery of Cima Dome and into Shadow Valley, along the tributary washes of Kelso Wash, and along alluvial slopes southeast of Baker. Banks and berms of washes are preferred places for burrows; such denning along washes, however, frequently results in significant mortality during flash floods. In July 1971, I followed the activity of tortoises in a wash north of Essex. Fifteen adult tortoises along 0.2 km of wash were drowned by flash flooding resulting from a downpour over uplands several kilometers distant. Subsequent reconnaissance of the area revealed that all burrows had been destroyed except one,

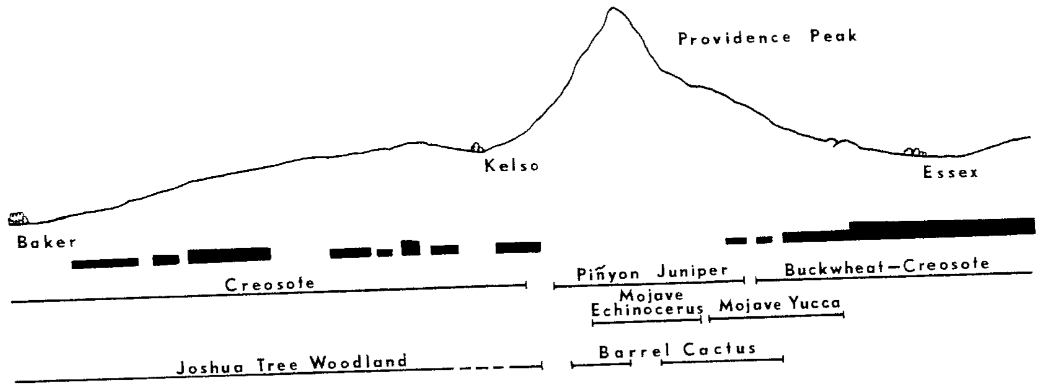

Fig. 10. Ecological transect of the Providence Mountains. San Bernardino County. Thickness of bars indicates relative tortoise densities encountered.

which contained three adult females. All the tortoises had been using shallow burrows in the banks of the wash.

A generalized transect across the Providence Mountains (Fig. 10) depicts the occurrence of tortoises in relation to elevation and vegetation in this region. The northern flank of the Providence Mountains supports higher tortoise population densities than do the southern flanks. The alluvium of the northern flank is sandy, whereas the southern flanks are covered by rocky aprons. The sandy areas around the nearby Kelso Dunes are surprisingly depauperate of tortoises. Considering the high-density areas near Hinkley (in the western Mojave) in similar habitat, this is an anomalous situation. A partial explanation may be the removal of tortoises by humans, because the area has long been a popular recreational site with easy access. Some mining activity in the area now threatens to expand to other portions of the dunes. However, even in areas of the dunes that have received little abuse, population densities of tortoises are low.

A similarly anomalous situation occurs in the Joshua tree woodlands in Lanfair Valley and on Cima Dome. Here the soils are composed of grus (derived from weathered granites) and can be excavated easily. Vegetation is diverse, and precipitation amounts to about 25 cm a year. Yet tortoise population densities appear to be lower than those at lower elevations in creosote scrub. Summer temperatures in Joshua tree woodland range from 2° to 3°C cooler than lower scrub areas, but whether this temperature difference is a limiting factor for tortoises is not known. Cattle grazing, which is concentrated in the higher regions (Joshua tree woodland), may affect tortoises. A comparative study of plots in low creosote scrub and in high desert should clarify these questions.

The highest tortoise densities I found in the eastern Mojave Desert were in the Fenner Valley, upper Ward Valley (Camino Valley), and portions of the Chemehuevi Valley (Figs. 3 & 9). All have friable substrates and are at relatively low elevations. Fenner Valley has sandy soils but displays little diversity of perennial scrub. Tortoises in this valley mostly frequent washes. In the other valleys substrates are either sandy or grus-like, and the diversity of the perennial scrub is great. The west side of the upper Ward Valley has a good admixture of perennial shrubs and is an area of extensive spring annual and fall grass development. The east side, along the alluvial apron of the Sacramento Mountains, is rocky and exhibits little scrub diversity. Interfluves are well-varnished pavements. Similar areas are found throughout the Chemehuevi Valley. Scattered in the Chemehuevi Valley, however, are pockets of friable sandy loams with good scrub growth that support high tortoise population densities.

Communications with local residents and the presence of abandoned burrows and shells indicate that some areas formerly supported large tortoise populations: the sandy area northeast of Twentynine Palms, the lower Ward Valley, and Rice Valley. Twentynine Palms has grown rapidly since the homesteading activities of the 1950's. Numerous "jackrabbit homesteads" dot the landscape. Roads, brush removal, off-road vehicle (ORV) use, and other human pressures apparently have drastically reduced the number of tortoises in this area. Rice Valley was the location of General Patton's World War II field maneuvers. More than 100,000 men were stationed there during the war years and extensive armored vehicle maneuvers were conducted, probably reducing tortoise numbers during this period. Tank and other vehicle tracks can still be found in Rice Valley, indicating the duration of ORV damage. North of Essex a similar military training center existed during the war years; however, since this was an infantry division, the overall impact was far less than that resulting from armored vehicle use in Rice Valley. Mining developments at Iron Mountain perpetuate human pressure in the lower Ward Valley.

During 1965, extensive war games were conducted over most of the eastern Mojave Desert in operation "Desert Strike." Thousands of men and hundreds of vehicles were involved. Tank pits, trash, and unexploded ordnance are still prominent in the landscape, and the activities of the military personnel no doubt had a serious and detrimental effect on the natural environment. Essex area residents reported that many dead tortoises were found after these maneuvers. Remarkably, in the western Fenner Valley, tortoises survived both the World War II maneuvers and the "Desert Strike" and have maintained healthy populations.

Construction and maintenance of railroad, highway, aqueduct, gas-line, and power-line corridors have repeatedly brought humans into contact with tortoises. Although cattle ranching is largely confined to higher elevations, it presents competition to tortoises in the Fenner and Granite Mountains. Feral burros are numerous in the Providence and Whipple Mountains (California DFG 1972). I found several tortoise burrows crushed by burro activities in the Woods Mountains. Burros compete with tortoises for forage, and during spring ephemeral blooms, burros forage in the Fenner and other valleys, denuding areas of vital tortoise food.

Children who lived in the small towns along Highways 66 and 95 once commonly collected tortoises to sell to tourists. Railroad section hands also transported tortoises found in the desert to stations in Needles and points east for promotional purposes or for sale to train passengers. Camp (1916) said of tortoises that "old ones are a favorite delicacy among Indians and Mexican section-hands who live with their families along the railroad lines." Most such encampments have now been abandoned. Further, the small towns along old Highway 66 became ghost towns after nearby Interstate 40 was completed in 1973. Pressure from local inhabitants has thus decreased because the human population of the area has recently declined.

The elevation of much of the eastern Mojave Desert is high and the terrain rocky or steep; few tortoises occupy such areas. Lake beds are essentially devoid of vegetation and tortoises. Most tortoises in the eastern Mojave occur in low-lying areas where there are scattered shrubs.

Colorado-Sonoran Desert

Tortoises apparently do not occur naturally west of the Salton Sea; this may be due to repeated Pleistocene flooding of the Salton Sea, a remnant of pluvial Lake Cahuilla. Tortoises are seldom seen in the low portions of the Salton Sink and are of only sporadic occurrence in the Orocopia and Chuckwalla Mountains. Populations occur at the Chuckwalla Bench and Cottonwood Mountain (Dimmitt 1977). Records from near Yuma, Arizona, are old, and the present status of tortoises in the southeastern corner of California is not well known. I located some tortoise populations in the Palen and Chuckwalla Valleys, and along the eastern and western flanks of the Chocolate Mountains. However, tortoise population densities in the Colorado-Sonoran Desert appear to be lower than those found in the Mojave Desert.

Ecology

Little is known about the ecology of the desert tortoise. Most of the information derives from a study of a Utah population by Woodbury and Hardy (1948). This study and other information on the natural history of the desert tortoise have been summarized by Pope (1939), Carr (1952), Stebbins (1954), and Ernst and Barbour (1972). A comprehensive bibliography for the genus *Gopherus* was given by Douglass (1975, 1977). Recently, Auffenberg and Franz (1978) listed selected pertinent literature for the species. Several ecological studies of this species by both university and government scientists are now in progress.

The Woodbury and Hardy (1948) study was of a desert tortoise population at the extreme northern limit of the range in southwestern Utah. Their findings portray behavioral adaptations of the animal in a continental climatic regime and are not broadly applicable to other populations. Attempts to apply the data known about the Utah population to other populations has led to misunderstanding and, in some cases, to mismanagement of tortoise populations. At the western margin of the tortoise range, an intensive ecological study is now being completed by R. W. Marlow for his doctoral dissertation; the study population, near California City in the western Mojave Desert, occurs in an area of relatively high rainfall, which may be responsible for higher densities here than elsewhere in the range. There is no "typical" tortoise population because of the great variation among local populations.

The following discussion summarizes the behavior and natural history of the desert tortoise, principally for California populations.

Activities

Daily activity patterns vary according to season. During early spring (March-April), tortoises usually emerge from their burrows in late morning. Once emerged and warmed, tortoises may be found on the surface throughout the remaining daylight hours, foraging or engaging in courtship. During summer, activity bouts become bimodal because daytime heat causes a cessation of aboveground activities from about 1000 to 1900 h. This pattern grades into a unimodal late morning to sunset pattern again in the fall (September-November). The desert tortoise is diurnal except, perhaps, during rare rainstorms that may trigger nocturnal emergence.

The spring emergence of desert tortoises is associated with the earliest prolonged warm period. In southern California under normal climatic conditions, this occurs in late February to early March, but the exact timing varies with geographic locality. Tortoises are voluntarily active at a wide range of body temperatures—19.8° to 38.3°C (Brattstrom 1965; McGinnis and Voight 1971). Thus, any warm day in midwinter can cause some animals to come out of dormancy for short periods of basking. A rise in tortoise activity coincides with increasing ambient temperatures and daily insolation. Peak activity occurs in the spring months when temperatures are mild and food is abundant in the form of newly sprouted ephemeral plants and their blossoms. Berry (1975) found that adult and juvenile activity patterns differ in that the time spent above ground by juveniles predominantly occurs during the peak of the spring ephemeral plant season. Adults and subadults may be active year-round, except for the winter dormancy period. In California, inactivity usually extends from October to February but depends on geographic location and climatic conditions. Certain Mexican populations may be active above ground all through the year (Auffenberg 1969), and certain California populations may be similarly active in mild years. Depending on the occurrence of late summer thunderstorms, a secondary peak of activity may take place in the fall. Although hatchlings emerge in the fall, they are seldom encountered then. Most young dig their own burrows or retreat into larger existing burrows.

Home ranges of adults varied from 0.4-4 ha in Utah (Woodbury and Hardy 1948) to 10-14 ha near the Desert Tortoise Reserve in the western Mojave Desert, California (Marlow 1974). Berry (1974a) reported that near China Lake, California, males have home ranges of 1.2-2.6 km^2, and females have slightly smaller activity areas. Similarly, Burge and Bradley (1976) reported that the mean home range of males might be somewhat larger than that of females. In southern Nevada, Burge (1977) found that the mean home range of 9 male tortoises was 32.3 ± 6 ha (range 11-65) and of 8 females, 14.8 ± 2.6 ha (6.4-27). Auffenberg (1969) indicated that some Mexican populations are nomadic. Hatchlings and juveniles restrict their activities to small home ranges usually associated with 1 or 2 burrows, and the radius of the juvenile home range may be 50 m or less (Berry 1975).

Tortoise Burrows

Burrows function primarily as thermoregulatory aids (Woodbury and Hardy 1948). They are warmer in winter and cooler in summer than the surrounding environment and usually have a higher and more constant humidity. The entrances may be plugged to increase the thermoregulatory advantage and to aid in water conservation. Burrows also provide protection from predators.

Burrowing habits of desert tortoises vary greatly in different geographic localities. Since temperatures in Mexico are generally mild in winter, a simple pallet (a scrape or depression, often under a bush) or a single shallow hollow apparently suffices for nocturnal shelter (Auffenberg 1969). However, Bury et al. (1978) found that some desert tortoises dig shallow burrows up to 1 m long for winter retreats on Tiburón Island, Sonora, Mexico. In northern and central Arizona, winter temperatures force winter dormancy, and hibernacula consist of burrows in the sides of arroyos that are deep enough to allow the posterior portion of the tortoise shell to be flush with the arroyo wall (Auffenberg 1969).

In southern Nevada, Burge (1978) defined four types of cover sites: den, burrow, pallet; and nonburrow. The average density of repeatedly-used cover sites (pallets and burrows) was 3.5/ha. Of 783 burrows and pallets, most (85%) were in soil with varying amounts of gravel; 72% were located under shrubs, and 26% were dug into banks or beds of washes. Individual tortoises (fitted with radio transmitters) used 12-25 cover sites each year, and most were used repeatedly. Other aspects of burrow design and use are presented in her paper.

At the extreme northern limit of the tortoise range in Utah, two distinct denning behaviors are evident—summer burrows and winter dens. Winter dens are the hibernacula and are usually horizontal tunnels 2-5 m long, but may be as long as 10 m (Woodbury and Hardy 1940, 1948). Winter denning sites are mostly in banks of washes, but they may also be located on flats or hill slopes. Auffenberg (1969) notes that these hibernacula are usually situated on south-facing slopes and are used communally. Emergence from the hibernacula is usually followed by migration to spring and summer foraging areas (Woodbury and Hardy 1948). Summer burrows are dug or old ones are cleaned out and used for nocturnal and diurnal shelter; they are shallow hollows, dome-shaped, up to 1 m long, and usually sunk at a downward angle. Most summer burrows are situated on flats and interwash areas, often under bushes, but they may also be found in the sides of washes. Animals return from foraging areas to dens in the fall. The ratio of summer burrows to winter dens in Utah averaged about 4:1 (Woodbury and Hardy 1948).

In most of California, there appear to be permanent deep burrows as well as shallow temporary burrows or pallets. The permanent burrow form that is found in most of southern California is about 1 m deep and sunk downward at an angle between 10 and 30° (Fig. 11). Marlow (1974) found that burrow depth near the Desert Tortoise Reserve seldom was greater than 3 m; the average was about 1 m. Deep labyrinth burrows similar to those found in Utah (Woodbury and Hardy 1948) are uncommon in California, but I found some near Hinkley in the western Mojave Desert (Fig. 12). A shallow burrow is usually constructed to be just deep enough to cover the tortoise (Fig. 11) and may occasionally be employed for periods of dormancy.

Fig. 11. Typical tortoise burrow under a creosote bush. Desert Tortoise Reserve, Kern County, California.

Adult tortoises in the Desert Tortoise Reserve usually have one to three permanent burrows and two to three shallow shelters or pallets (R. W. Marlow, personal communication). Burrow size is directly related to size of the individual tortoise. The location of each burrow and distance to the burrow apparently is known by each animal, since some tortoises on long forays return to the same burrow at the termination of activity.

Often during the summer, California desert tortoises may simply seek shelter of a bush and scrape a small depression (pallet) beneath it for shelter; this behavior resembles that of *Gopherus berlandieri* in Texas (Auffenberg and Weaver 1969) and of Mexican populations of *G. agassizii* (Auffenberg 1969). Berry (1972) has suggested that an adult tortoise may accrue a thermal advantage by spending the summer or spring night above ground in the open. At night, surface soil and air temperatures drop to 20-24°C. The body temperature of a tortoise in the open would be similar. Air temperatures in a burrow 1-1.2 m deep may remain between 30 and 34°C. Thus a tortoise that spent the night in the open under a bush or in some other

Fig. 12. Large deep burrows in side of wash. Near Hinkley, San Bernardino County, California.

type of pallet could start the morning with a body temperature 1-6°C cooler than one that spent the night in a burrow. Since a longer time is required to reach the critical maximum temperature (Brattstrom 1965; McGinnis and Voight 1971), a longer period of activity may be possible in the morning. However, Cowles and Bogert (1944) showed that when desert reptiles become active in the morning, they can quickly increase their body temperatures to the preferred level. Further, Bury (1972) has shown that in the emydid turtle (*Clemmys marmorata*) the increase in body temperature from the time of emergence (about 18°C) to a preferred level (30-32°C) takes only about 30 min. Thus, a tortoise emerging from a burrow and one that spent the night above ground would probably reach the preferred body temperature at about the same time and would behaviorally maintain that level throughout the day. Tortoises may remain on the surface at night because of cooler ambient temperatures, which would maintain body temperatures at lower levels for the night. Such a preference for low temperatures may be important to reduce the rate of metabolism.

Commensals

A number of animal species have been noted in a commensal relation with tortoise burrows, especially those of *Gopherus polyphemus* (Carr 1952; Brode 1959; Blair and Kilby 1936; Young and Goff 1939). Existence of commensals within *G. agassizii* burrows has generally not been acknowledged or has been deemed unimportant (Grant 1936). Since underground shelter in the desert is limited, tortoise burrows represent places for many animals to escape predation and extremes of heat, cold, and dryness. Some species are found repeatedly in association with tortoises. Woodbury and Hardy (1948) commented that a large number of animals used *G. agassizii* burrows in Utah, and Burge (1978) noted use of burrows by other species in Nevada.

In the Stoddard Valley of western San Bernardino County, I found three burrow complexes occupied by tortoises and Burrowing owls (*Athene cunicularia*). Each complex consisted of 6 to 11 burrow openings, of which 3 or 4 were used by tortoises and the remainder by the owls (Fig. 13).

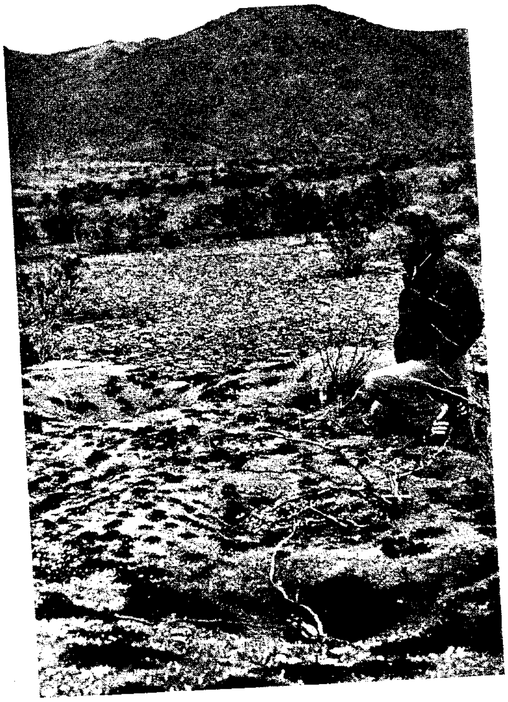

Fig. 13. Complex burrow system south of Barstow, San Bernardino County, California. Burrows are occupied by tortoises, burrowing owls, and antelope ground squirrels.

Ground squirrels used some of the burrow complexes. I have flushed Poorwills (*Phalaenoptilus nuttallii*) from other tortoise burrows during the summer; the burrows may serve as hibernacula for Poorwills during the winter months. I observed Black-tailed jackrabbits (*Lepus californicus*) using tortoise burrows or pallets for resting and for escaping from summer heat. Rattlesnakes frequently occur in tortoise burrows in the Fremont Valley, notably the Mojave rattlesnakes (*Crotalus scutulatus*). Sidewinders (*C. cerastes*) also frequent tortoise burrows, but they usually use shallow pallets. Black widow spiders (*Latrodectus mactans*) build orbs inside larger tortoise burrows. Animals known to be commensals of the desert tortoise are listed in Table 2; no obligates, however, have yet been noted.

Diet

The desert tortoise is herbivorous. The most important foods of California tortoises apparently are desert annuals, plants that often have a life span of less than 30 days. Both flowers and vegetative portions are eaten, although during the peak of flowering I have observed that flowers are preferred. On 7 July 1973, I watched an adult tortoise at Hinkley forage exclusively on annuals for 3 h. I have observed tortoises eating the plants that are listed in Table 3.

Peak tortoise activity usually coincides with the abbreviated period of annual bloom. During the spring bloom, tortoises apparently consume enough annual forage to sustain them through the summer aestivation and winter dormancy periods.

Table 2. *Commensals of the desert tortoise and its burrows. Sources: 1, Utah (Woodbury and Hardy 1948); 2, Nevada (Burge 1978); and 3, California (this study).*

Common name	Scientific name	Source
Ticks	Acarina	1,2
Black-widow spider	*Lactrodectus mactans*	2,3
Tarantula	*Aphonopelma* sp.	2
Silverfish	Thysanura	1,2
Roaches	Orthoptera	1,2
Ant lions	Neuroptera: Myrmeleontidae	1
Ground beetles	Coleoptera: Tenebrionidae	1-3
Tarantula hawk	*Pepsis* sp.	2
Desert spiny lizard	*Sceloporus magister*	1
Zebra-tailed lizard	*Callisaurus draconoides*	3
Desert iguana	*Dipsosaurus dorsalis*	3
Side-blotched lizard	*Uta stansburiana*	3
Whiptail lizard	*Cnemidophorus tigris*	3
Banded gecko	*Coleonyx variegatus*	1
Coachwhip	*Masticophis flagellum*	1,2
Gopher snake	*Pituophis melanoleucus*	1
Spotted night snake	*Hypsiglena torquata*	1
Western rattlesnake	*Crotalus viridis*	1
Mojave green rattlesnake	*Crotalus scutulatus*	3
Sidewinder	*Crotalus cerastes*	1-3
Poorwill	*Phalaenoptilus nuttallii*	3
Burrowing owl	*Athene cunicularia*	2,3
Pocket mouse	*Perognathus* sp.	2,3
Canyon mouse	*Peromyscus crinitus*	1
White-footed mouse	*Peromyscus* sp.	2
Kangaroo rat	*Dipodomys merriami*	2,3
Desert woodrat	*Neotoma lepida*	1-3
Antelope ground squirrel	*Ammospermophilus leucurus*	2,3
Desert cottontail	*Sylvilagus auduboni*	1,3
Black-tailed jackrabbit	*Lepus californicus*	1-3
Kit fox	*Vulpes macrotis*	2,3

Table 3. *Some plant foods of the desert tortoise in California.*

Common name	Scientific name
Broadflowered gilia	*Gilia latiflora*
Gilia	*Gilia* sp.
Brown-eyed primrose	*Oenothera clavaeformis*
Primrose	*Oenothera* sp.
Dapple-pod locoweed	*Astragalus lentiginosus*
White mallow	*Malvastrum exile*
Yellow peppergrass	*Lepidium flavum*
Lacy phacelia	*Phacelia tanacetifolia*
Phacelia	*Phacelia* sp.
Tansy mustard	*Descurainia pinnata*
Checker fiddleneck	*Amsinckia tessellata*
Ghost flower	*Mohavea confertiflora*
Verbena	*Abronia* sp.
Plicate coldenia	*Coldenia plicata*
Yellow comet	*Mentzelia affinis*
Blazing star	*Mentzelia albicaulis*
Desert star	*Monoptilon bellioides*
Pincushion flower	*Chaenactis Fremontii*
Wild daisy	*Erigeron* sp.
Coreopsis	*Coreopsis Bigelovii*
Eriophyllum	*Eriophyllum Wallacei*
Paperflower	*Psilostrophe Cooperi*
Desert dandelion	*Malacothrix glabrata*
Yellow saucers	*Malacothrix sonchoides*
Desert marigold	*Baileya* sp.
Desert chicory	*Rafinesquia* sp.
Glyptopleura	*Glyptopleura setulosa*
Creosote	*Larrea tridentata* (seeds)
Ricegrass	*Oryzopsis hymenoides*
Schismus grass	*Schismus* sp.
Galleta grass	*Hilaria rigida*
Brome grass	*Bromus rubens*
Storksbill	*Erodium cicutarium*

Forage must also be sufficient to allow the female to accumulate energy reserves for egg production. In dry springs, tortoises may rely on fat reserves accumulated during the previous spring. This phenomenon has been observed in other reptiles (Hahn and Tinkle 1965). Berry (1974*b*) reported that egg laying by the large herbivorous lizard *Sauromalus obesus* ceased in drought years. Because tortoises are large herbivorous reptiles, they might be expected to respond to reduced forage during drought conditions similarly by foregoing egg laying. Such a response would be typical of animals characteristically large-bodied, long-lived, and slow to mature, and that have low recruitment rates.

Grasses are mostly secondary food items and are probably used only to maintain summer activity. Dried grasses and dried annuals are normally the only food available during the late summer (July–September). In some areas, late summer thunderstorms can initiate a secondary germination of desert plants and thus induce localized secondary peaks of tortoise activity. Such late summer rains cause the appearance of "6-week grasses" such as foxtail chess (*Bromus rubens*) and chinch weed (*Pectis papposa*). Although Woodbury and Hardy (1948) seem to have overemphasized the role of grasses as a food source, all their observations on feeding behavior were made from September to November and in January, when the only plant material available was grasses.

Food habits of tortoises in northern Arizona and southern Utah were investigated by scat analysis by Hansen et al. (1976). They found that three species of grasses (*Aristida, Tridens,* and *Bromus*) accounted for 61% of the diet. However, since the collection of scats was not identified by season, the samples may have been biased for certain food items (such as grass parts) that produce lasting scats. Further, they found little regional variation in diet.

Since forage availability influences activity patterns, Mexican and southern Arizona populations may be active year-round in response to warmer winter temperatures and the availability of year-round forage (Auffenberg 1969). Some geographic variability in feeding patterns is apparent in California tortoises. In the northern Mojave Desert, schismus grass (*Schismus* sp.) has not been reported as eaten by tortoises (Berry 1972, 1974*b*, 1975); yet in the eastern and central Mojave, I have observed that *Schismus* is commonly eaten, particularly during late summer months.

With the exception of prickly pear pads (*Opuntia basilaris*), I have never observed a desert tortoise feeding on the vegetative portions of desert perennials. Their avoidance of these plants is probably related to the high salt content. In this respect, tortoises are similar to chuckwallas (*Sauromalus obesus*), which apparently eat only annuals, grasses, or the flowers of shrubby perennials (Berry 1974*b*), and die if they are force-fed leaves from certain perennial shrubs (Nagy 1972, 1973).

In a Nevada population studied by Burge and Bradley (1976), tortoises were observed eating seven different species in the shrub layer. The shrub species most frequently used were desert mallow (*Sphaeralcea ambigua*) and ratany (*Krameria parvifolia*). Tortoises also ate the terminal growth buds of pencil cholla (*Opuntia ramosissima*) and, seasonally, prickly pear pads. The most important dietary item was common plantain (*Plantago insularis*), which was eaten throughout the year. Hansen et al. (1976) noted that although food of Utah and Arizona tortoises consisted of a variety of grasses, sedges (*Carex* sp.), and forbs and shrubs, generally only the succulent portions such as leaves and flowering parts were eaten. They also found sand, bird feathers, mammal hairs, snake and lizard skin, and arthropods in some scats.

Desert tortoises in captivity eat a wide variety of foodstuffs including meat (Nichols 1953; Ernst and Barbour 1972). I examined about 200 scats in the field during 1973, of which only two contained any animal matter, and both were beetles (one *Cryptoglassa* sp. and one unidentified tenebrionid that could have been ingested accidentally).

Both captive and wild animals have been observed eating small amounts of sand. Frequency of sand ingestion appears to increase towards the end of summer and in early fall. Scats excreted at this time may be composed almost entirely of sand. I have also found sand in the large intestine of several autopsied specimens. Geophagy has been reported from a number of other chelonians (Sokol 1971; Kramer 1973). The function of soil in the diet of tortoises is not known, but it may be an aid in digestion, and such scats may serve as territorial or individual markers.

When tortoises forage, they wander from plant to plant, stopping briefly to put their noses to the ground or the plant. Head bobbing often accompanies this exploration (Eglis 1962), and olfaction apparently is involved (Weaver 1970). Both males and females have well-developed integumentary glands on their chins; these tend to be larger in males. Although I have spent much time observing tortoise activity and have never knowingly witnessed scent-marking, I believe it to be a distinct possibility. Such marking could play a role in foraging or in delineating home range. Its function need not be territorial; it could be valuable simply as an aid to locate the tortoise's activity space, and it may be used in sex recognition. Weaver (1970) reported that sniffing by *G. berlandieri* occurred in nearly all the combat and courtship encounters he observed. Chin gland secretions are different in each *Gopherus* species (Rose et al. 1969; Rose 1970).

A special posture is used in thermoregulation and, presumably, to aid in digestion by increasing the body temperature. The tortoise lies spread-eagled in the sun or under a bush, with limbs and neck extended and limp. Sleeping individuals were frequently seen lying in this manner after active foraging.

Water Metabolism

Standing water is seldom encountered by tortoises. Desert springs are usually located in steep, rocky terrain that is often inaccessible to tortoises. However, free-living tortoises in desert flatlands may drink from shallow depressions, some of which are dug and expanded by tortoises (Nagy and Medica 1977; Medica et al. *in press*). Home range familiarity allows the animals to locate rainfall puddles in these catchments and natural depressions. Specific boulders with depressions where water persists after rains are well known and widely used. On three occasions, I observed individuals licking moisture from rocks. Wild individuals may come to puddles left on asphalt roadways following rains. Where groundwater is close to the surface, the density of tortoises increases. For example, tortoises were abundant along the Mojave River before agricultural pursuits changed the habitat (Stebbins 1954).

Tortoises may subsist on water derived from food and metabolic pathways (Stebbins 1954; Auffenberg 1969). Leopold (1961) reported that water is stored in two "sacs" under the carapace. These sacs constitute a bilobed urinary bladder, and may contain large amounts of urine.

Dantzler and Schmidt-Nielsen (1966) demonstrated that the desert tortoise is capable of withstanding considerable dehydration and can tolerate large increases of ion concentrations in its blood plasma. They also found that the kidney remains functional even during mild dehydration and that nitrogenous wastes are stored in the bladder; these walls are more permeable to water in the desert tortoise than are those of freshwater turtles. Wastes are precipitated in the bladder as semisolid urates. When water is available, urine is not reabsorbed by the bladder but is excreted as dilute urine. But tortoises apparently are also able to go for months without discharging urine from the bladder. Approximately equal amounts of urea and uric acid were excreted by the *G. agassizii* examined by Dantzler and Schmidt-Nielsen (1966).

Evaporation from the integument constitutes a major source of water loss from desert tortoises, with respiratory loss secondary in importance. However, both types of water loss are much less than that of turtles found in damper climates. Thus, cutaneous water loss in *G. agassizii* at 23°C is 1.5 mg/cm^2 per day, compared with 5.3 mg in the box turtle, *Terrapene carolina* (Schmidt-Nielsen and Bentley 1966). Water conservation also occurs in the egg shell, which is resistant to water loss (Stebbins 1954).

Minnich (1976, 1977) measured water turnover rates in a desert tortoise population in the Mojave Desert. He found that the rates during most of the summer of 1970 were exceedingly low (0.36 mL/100 g per day) and only slightly greater than rates of water metabolic production (0.31 mL/per day). During the summer period, osmotic pressure of the bladder urine increased steadily until it equalled that of the plasma, suggesting that as the tortoise dehydrates it reabsorbs water from the bladder. After one rainfall of 1.2 cm, tortoises drank rainwater (an average of 14.4 mL/100 g of body weight), gained weight, and produced a dilute urine that was stored in the bladder.

Urine and large amounts of semisolid urates are frequently voided during handling. Patterson (1971) reported that tortoise urine could pucker the mouth of a kit fox. Thus, urination may serve as a predator defense. Handling often causes urination and may represent a severe water loss to the tortoise, particularly to juveniles. Proper handling techniques can eliminate this danger. Folding the tail over the cloaca by placing a finger between the carapace and plastron often prevents a tortoise from urinating.

Reproduction

Mating starts with spring emergence of the tortoises and may continue until the fall dormancy period. I observed mating in August near Hinkley in the western Mojave Desert, and Berry (1975) noted mating as late as October at China Lake. Peak breeding activity, however, is in spring (March–June). Males often approach one another and fights ensue. When courting, a male approaches a female with head and neck extended and head bobbing. The male then proceeds to bite and nip the female's head and forelimbs or the edge of the carapace. Ramming and circling by the male often occurs. The male mounts from the rear and, by standing on the tips of his front claws, is able to bring his shell into a nearly vertical position. Urination may occur at this time, but its significance, if any, is not known. Much grunting, stretching of limbs, and rhythmic humping is typical of male activity (Weaver 1970). Tortoises may be surprisingly vocal during mating. Campbell and Evans (1967) reported two types of sounds—a grunt and a drawn-out moan. Patterson (1973) recorded numerous vocalizations, some of which sound like baying hounds.

Nesting occurs mainly from May through July. Captive individuals have nested as late as October and often have two or three clutches per year (Stewart 1954; Miller 1955). Some wild individuals may also have multiple clutches, and late nesting may explain the overwintering of eggs reported by Grant (1936).

Tortoises dig nests in sandy or friable soil by using the hind feet or by first using front legs, then hind legs. When both are used, the female first digs a broad, shallow hole with the front legs and then backs into this hole and digs with her rear feet (Booth 1958; Edell 1970). Measurements of a nest given by Nichols (1953) were about 23 cm (9 in.) in diameter at the top, 18 cm (7 in.) in diameter at the bottom, and 15 cm (6 in.) deep. Occasionally, eggs are deposited singly and at random sites (Miller 1932). The nesting cavity may be dug in the mouth of a permanent burrow.

Observations of nest construction by captive tortoises suggests that the depth of nests varies with the length of the female as well as with the hardness of the soil. Females apparently construct nest sites that resemble undisturbed ground and usually urinate in the nest before or after filling it.

After nesting, females appear to be less active above ground than males. Males remain above ground longer than females and apparently remain sexually active throughout the summer. Of 124 individuals I examined in the field during August 1973, 80% were adult males.

Eggs vary from elliptical to nearly spherical, with a dull, chalky color and rough texture. Of 19 eggs that I measured, the average dimensions were 47.9 mm long and 39.0 mm in maximum width (37.6 mm in minimum width). Average egg weight was 33.6 g; similar weights were reported by Grant (1936) and Miller (1932).

Clutch size varies from 2 to 14 eggs; 5 or 6 is the typical number (Grant 1936; Ernst and Barbour 1972). Clutch size is related to the size of the female, with larger females generally having larger clutches—a phenomenon also found in other species of reptiles (Fitch 1970).

In the wild, incubation apparently varies from 90 to 120 days. An incubation period of 118 days was noted by Grant (1936) for eggs of animals in captivity. Artificially incubated eggs usually hatch in 80-90 days (Lampkin 1966; Shade 1972). For tortoises in captivity, an 80% hatching rate is considered high; hatching success of 60% or less is more common. Failure of some artificially incubated clutches may be due to high constant temperatures maintained in incubators. At hatching, the yolk sac remains attached in the center of the plastron, but it is rapidly absorbed. The yolk sac is about one-third the size of the hatchling tortoise and greatly impedes locomotion for the first few hours of life.

Hatching generally occurs from August to October; some eggs apparently overwinter, and hatchlings appear in the following spring. Little food is available at the time of most hatching in late summer, and hatchlings spend little time on the surface. Hatchlings dig their own small burrows, or use an existing larger burrow. Dormancy shortly follows, probably before the hatchling has eaten or taken a drink. My observations of hatching in captivity suggest that food is ignored between the time of emergence and the beginning of dormancy.

Growth and Maturation

Hatchlings are nearly as wide as they are long. The shell is soft and remains soft for 5 to 10 years; during this time, the hatchlings are very susceptible to predation. The shell of the young is generally dull yellow and the edges of the scutes are brown, a cryptic color pattern that merges well with the late summer aspect of the desert. Hatchlings are pugnacious and will butt at anything that moves.

Sexual maturity of the desert tortoise in the wild apparently is reached at a carapace length of 230-265 mm, between 15 and 20 years of age (Woodbury and Hardy 1948). Berry (1975) reported that females may mature at a carapace length of 215-220 mm. With regular feeding for two-thirds of the year, tortoises in captivity may reach maturity at 12 to 13 years of age (G. R. Stewart, quoted in Berry 1975). Growth rates of captive tortoises are given by Patterson and Brattstrom (1972). Accelerated growth rates and early maturity ascribed to year-round activity and continuous high-quality nutrition have been reported for captive animals (Jackson et al. 1976). Medica et al. (1975) reported that the growth rate in tortoises in Nevada was related to environmental conditions; growth was greatest following winters of high precipitation. Immature animals (less than 200 mm in plastron length) increased from 1.8 to 12.3 mm per year ($\bar{x}$ = 9 mm) over a 5-year period. Under natural conditions, the feeding period lasts only from 6 weeks to 3 months in good forage years, which occur on an average of once in 5 years. Thus, growth and maturity are often delayed in the wild.

Population Structure

At China Lake, California, a tortoise population was composed of 2% hatchlings, 8% juveniles (1-10 years old), 31% subadults, and 59% adults, when a carapace length of 215-220 mm was used as the criterion for the adult age class (Berry 1975, 1976). The sex ratio was 1.78:1 in favor of females. Similarly in the Fremont Valley, 2% of a marked population were hatchlings, 56% were juveniles and subadults, and 42% were adult (Marlow 1974). Burge and Bradley (1976) found similar percentages (55% adults, 44% juveniles and subadults, 1% hatchlings) in a tortoise population in Nye County, Nevada.

The Utah tortoise population on Beaver Dam slope reported by Woodbury and Hardy (1948) consisted of 90% adults. In adults, the sex ratio was 1.51:1 in favor of females. Since 1945 this Utah population has experienced a drastic decline, from 59.5 individuals/km² to 10.4/km² and a reversal in sex ratio (2.33:1) in favor of males (Coombs 1977).

Natural Mortality

It is common for 50% of a clutch from desert tortoises in captivity to be infertile (Lampkin 1966), and similar losses may occur in the wild. Surviving juveniles apparently maximize their chances of reaching maturity by spending little time above ground. Juveniles emerge in the spring to bask and forage, but they return to their dens when the ephemeral annual plants wither. Thus, juveniles may spend less then two months of the year above ground. Adults are potentially active on the surface nine months each year in California, albeit at varying levels of activity.

Of the 281 animals (90% adults) that were marked in Utah over a 10-year period (Woodbury and Hardy 1948), the remains of only 30 animals were found and the mortality estimated at 1% per year. Berry (1972, 1975) reported similar rates of less than 5% mortality per year in a tortoise population in the western Mojave Desert. The rate for these long-lived animals was low, as expected.

The coyote (*Canis latrans*) is common throughout the desert and is a major predator of tortoises. Coyotes are persistent and chew on the limbs and carapaces of tortoises for extended periods, and they often return to pursue a tortoise left earlier (Berry 1972). Coyotes may also dig tortoises out of their burrows, excavating behind the burrow entrance (Berry 1972). During field surveys (see Appendix), I encountered large numbers of tortoise carcasses, for many of which coyotes were apparently responsible. When tortoise remains are found, however, it is not always possible to distinguish the results of active predation from those of scavenging. It is not uncommon to find tortoises with scarred or cracked shells and damaged or amputated limbs (or both), which are likely indications of attempted predation by carnivores. Overall, the coyote may be an inefficient predator on adult tortoises because so much energy is expended in an attempted kill.

Badgers (*Taxidea taxus*) are more common in the desert than is generally recognized and can easily open an adult tortoise. Bobcats (*Lynx rufus*), skunks (*Spilogale putorius* and *Mephitis mephitis*), and kit foxes (*Vulpes macrotis*) may prey on both eggs and tortoises. However, since most of these animals are nocturnal, they encounter tortoises infrequently. These carnivores could dig out smaller tortoises. Robert Mallette of the California Department of Fish and Game (personal communication) has found hatchling tortoises to be a major food item of a pair of Golden eagles (*Aquila chrysaetas*) during the nesting season in the Mojave Desert. Other avian predators on small tortoises probably include Red-tailed hawk (*Buteo jamaicensis*), Holarctic raven (*Corvus corax*), Burrowing owl (*Athene cunicularia*), and roadrunners (*Geococcyx californianus*). Coachwhip snakes (*Masticophis flagellum*) are capable of taking both eggs and juvenile tortoises, and the Gila monster (*Heloderma suspectum*) is a known predator also (Hensley 1950).

One of the most important limiting biotic factors on desert tortoise populations is probably predation. Predation on the small-sized juveniles would be expected to be high and remains are usually not found. This loss, combined with the possible low fertility and with predation on eggs, probably accounts for the small percentages of hatchlings and small tortoises found in the wild.

Tortoise populations today may be expanding (or have expanded) as a result of predator control programs in the southwestern deserts. Most such programs have recently been discontinued, and predators are again increasing. Consequently, tortoise populations may be approaching a new equilibrium with expanding predator populations.

Flash flooding during the summer months occasionally causes the loss of animals denning in washes. I have observed such mortalities in both the Fenner and Fremont Valleys; flooding can wipe out local populations.

Overturned tortoises probably result from fighting or predation. A tortoise in this position is rarely helpless; only if the substrate is hard or if the animal is weak or deformed will it be unlikely to right itself. If a tortoise remains overturned in direct sunlight for any length of time, however, it becomes vulnerable to overheating. When its body temperatures exceeds 39.5°C, a tortoise suffers thermal stress and may die if not quickly removed to a cooler environment.

The adobe tick (*Ornithodorus turicata*) is known to parasitize *G. agassizii* (Harbison 1937; Ryckman and Kohls 1962). I have found infestations to be common in the Hinkley population, although individuals did not appear to be weakened by the ticks. The effects of tick infestation are not known. Occasionally a bone disease occurs in the desert tortoise which causes loss of scales and scutes (Miller 1932; Frye 1973); the disease is generally fatal.

Woodbury and Hardy (1948) reported that occasional grass fires kill tortoises in Utah. Such fires, however, are rare in the California desert.

It is my conclusion that the most significant cause of mortality today is human activity. The same conclusion was reached by Auffenberg and Weaver (1969) in their studies of *G. berlandieri* in southeast Texas. This cause of mortality is discussed below.

Conservation

Human Impact

Historical Depredation

Human pressures have been a factor affecting desert tortoise populations for thousands of years. Although the Mohave Indians specifically avoided the use of turtles as food, neighboring Chemehuevi and other Piutes ate them (Kroeber 1925). Tortoises were used for food, bowls, scrapers, rattles, decorations, trade and barter items, and as pets. However, such pressure on tortoise populations was probably minimal because native Indian populations were small and seminomadic. Many more tourists may be in the desert on one winter weekend now than there were resident Indians historically.

Collection and Removal

Until recently, the most important human activity affecting the distribution and abundance of desert tortoises has been direct removal, despite the longstanding law that prohibits harming, collecting, or removing tortoises from areas in California. In the spring, when most people visit the desert, tortoises are above ground in large numbers and are easily captured because they are slow-moving and diurnal.

In the spring of 1973, temperatures in the Mojave Desert were mild, and publicity about the flower displays attracted large numbers of tourists to the desert. The following autumn, many *G. agassizii* were brought to the Alexander Lindsey Junior Museum of Walnut Creek near San Francisco. During October, 45 tortoises were presented to the museum. Evidently, many local residents had visited the desert during the spring of 1973, and many had brought tortoises back with them. Acquistion of captive tortoises by this means is a seasonal event at most of the Bay Area nature centers and museums, but the numbers of individuals involved during 1973 were unusually high.

A survey by the International Turtle and Tortoise Society reported a minimum number of 23,000 turtles and 6,500 tortoises kept by its members (Anon. 1971); no geographical breakdown is given, but the Society's California chapter is the largest. Further, 75% of the above totals were species native to the members' area. Because there are only two native chelonians in California (the other is the Western pond turtle), the desert tortoise comprised a significant percentage of all such pets. *Gopherus agassizii* is a common pet throughout the United States and, formerly, could be bought in department and pet stores. If one of every 100 families in Los Angeles County had a pet tortoise, there would be 20,000 tortoises in Los Angeles. The densities of tortoises in some metropolitan counties (Los Angeles, Orange, Riverside, Contra Costa) probably are comparable to densities found throughout most of the California desert. There is also a sizeable backyard accumulation of tortoises in Bakersfield, California (R. Marlow, personal communication). Similarly, Keasey (1971), writing of Tucson, Arizona, said, "Because of their hardiness and reproductivity [sic] in captivity, the population of backyard tortoises in this desert city is only a little short of phenomenal."

Since the study by Woodbury and Hardy (1948), the Utah population has declined from a known population of about 300 to only 40 individuals. The location of the site is well known and is visited several times each year by field trip groups from numerous colleges and universities. Furthermore, these animals are occasionally collected, although the desert tortoise is now protected in Utah. Representatives from schools as far away as the Atlantic seaboard stop by annually on collection trips (Coombs 1974). Coombs (1974, 1977, and personal communication) stated that this type of collecting pressure has been one factor in reducing tortoise numbers on the Beaver Dam slope in Utah.

Illegal trafficking for commercial purposes is also a major cause of depletion. Although few people are involved in commercial traffic, the total number of tortoises is probably similar for commercial and private removal. Captured specimens of desert tortoises were once distributed worldwide. Improved enforcement apparently is curtailing such removal to some extent. One arrest was made of a California dealer in 1970, a case involving the illegal collection of 290 animals (Bury and Marlow 1973). Chambers of Commerce of desert communities have repeatedly used tortoises for promotional purposes in the past.

Railroad section workers once sold many tortoises to train passengers. Railroads also collected them for promotion and display at their stations, such as in Needles and Kelso. These activities have ceased.

In California, pets are frequently liberated, occasionally on a large scale. Before 1969, the California Department of Fish and Game (DFG) was releasing about 50 tortoises per year (Stewart 1973), some of which were *G. berlandieri*. In 1973, the DFG released 259, for which they kept records (J. St. Amant, memorandum, 16 April 1973). Between 1969 and 1972, G. R. Stewart and his students released 248 tortoises (personal communication). Mortality of these released animals is presumed to have been high. Kristin Berry (personal communication) suggests that mortality is related, in part, to the length of time tortoises are retained in captivity. Further, Stewart (1973) notes that though many tortoises consume native foods while in captivity, they fail to develop and use natural defense reactions. At first, released tortoises are not mobile and appear to wait, expecting to be fed. Potential dangers of liberating pets include the introduction of diseases (such as influenza, bone disease, or other epizootics), gene pool mixing, disruption of social structures, and introduction of exotic species. Most release programs have been stopped.

I strongly advise against the release of captive tortoises to the wild, except for special instances when the animal is unaccustomed to captivity (recently caught) and can be returned to the exact site of capture within a few months. The California DFG has a program to rehabilitate tortoises for possible reintroduction to depleted areas (St. Amant 1977); it can also authorize a permit for keeping tortoises that have been in captivity for long periods. If an animal is no longer desired as a pet, the assistance of the California DFG (or a comparable agency in other states) should be requested. The California Turtle and Tortoise Club also accepts tortoises for their adoption program (Lewis 1977).

Berlandier's tortoise occurs in Texas and northern Mexico, where it is protected. However, many *G. berlandieri* have been imported into California for the pet trade, mostly from northeast Mexico through New Mexico to avoid Texas laws (Brame and Peerson 1969). Auffenberg and Weaver (1969) reported that 4,000 *G. berlandieri* were collected for one shipment. Glenn R. Stewart (personal communication, 1974) mentioned one shipment of 8,000 animals transported in two vans and estimated that some 40,000 *G. berlandieri* were being imported to California each year. The California DFG attempts to regulate trafficking in *G. berlandieri* and *G. agassizii*; the sale of both species is now illegal in California. Many shipments have been confiscated, but most animals have been released later. Differences between *G. berlandieri* and *G. agassizii* present a problem of recognition for nonspecialists; frequently *G. berlandieri* is sold as "Gopherus" or "desert tortoise." In 1970, G. R. Stewart (personal communication) found the remains of a *G. berlandieri* near Palm Desert, Riverside County; other specimens have also been observed in the desert by his students. About 20% of the tortoises turned into the Alexander Lindsey Junior Museum in Walnut Creek, California, are Berlandier's tortoise, which indicates how common they were on the commercial market.

Impact of Traffic and Off-road Vehicles

Decreases in tortoise populations due to direct contact with humans will increase as the desert becomes more popular and accessible for recreation. During movements and foraging, tortoises cross roads where they may be collected by people seeking a pet or killed by passing vehicles (Fig. 14).

Fig. 14. Two adult tortoises killed by vehicles on a road near California City, California (Photo by R. W. Marlow).

Nicholson (1978) found that vehicular traffic on paved roads has a detrimental effect upon tortoise populations within about 1 km of the road, and that such roads may be a major factor contributing to the reduction of tortoise populations.

Human activity in the desert has a second major impact on tortoise populations. Nearly everyone who now visits the desert comes to drive over it. Every sort of off-road vehicle (ORV) is used: dune buggies, motorcycles, mini-bikes, motorized tricycles, all-terrain vehicles, sail planes, and four-wheel drive (4WD) vehicles. There has been a great increase in visitation in recent years. Recreational use of the California Desert in 1958 was estimated by the BLM (1968) to be 4.9 million visitor-use days (defined as one person spending 12 h). The total in 1973 was 13 million and the trend continues (Carter 1974). This massive increase in the influx of visitors increases the chances for direct removal of tortoises by collecting. About 1 million motorcycles are owned by Californians for off-road use; dune buggies number about 200,000, and 4WD's number about 500,000. Organized ORV events are held almost weekly through the fall, winter, and spring, attracting thousands of participants. Although the BLM recognized the need to regulate their use, control of ORVs has been minimal. Not until 1972 did the BLM begin to require that special land-use permits be obtained by organizers of competitive events. Between September 1972 and September 1973, 151 such events were held in California deserts, involving more than 67,000 participants (Carter 1974), and many more were held without permits. Some ORV users often travel by themselves.

Off-road vehicle use on the California desert has already had significant effect on the distribution and abundance of tortoises. In 1974–75, Bury et al. (1977) found 18 tortoises on 8 unused areas (2 ha each) but only 5 tortoises on 8 ORV-used sites. In 1976–77, we censused two 25-ha sites of similar terrain near Barstow, San Bernardino County; 34 tortoises were found in the control area but only 15 in the ORV-used area (Bury 1978; Bury and Luckenbach, unpublished data). The estimated tortoise biomass was 3.4 kg/ha in the control area and 0.5 kg/ha in the ORV-used area. In the control area, 171 burrows (51% actively used) were found versus 62 burrows (35% actively used) in the ORV area. Adult tortoises apparently were removed or killed in the ORV area. Off-road vehicles also collapse tortoise burrows. In general assessments, Berry (1973) and Bury et al. (1977) concluded that a pronounced detrimental effect on the desert ecosystem results from ORV use. Such effects are widespread and enduring, if not permanent (Stebbins 1974; Luckenbach 1975).

Growth of annuals and herbaceous perennials is severely reduced by ORV activity (Luckenbach and Bury, *in press*), and the basic energy fixation and transfer systems of the desert are disrupted or destroyed by vehicular activity. For example, insects and arthropods are important in pollinating desert plants as well as in conditioning desert soils; they, in turn, are food for lizards, snakes, rodents, birds, and carnivores. Because tortoises are herbivorous, they respond immediately to disruption of the food web.

Impact of Grazing

Grazing has been suspected as a factor detrimental to tortoise populations (Bury and Marlow 1973). Marlow (1974) pointed out that sheep eat many of the same plants as tortoises but that sheep are better competitors for food resources by virtue of their larger size, more efficient dentition, and greater mobility. Because they are trailed in large flocks, sheep can consume nearly all of the spring forage in an area. Marlow (1974) states that he counted 23 pallets and 4 tortoise burrows trampled by a flock of sheep in a 10-ha area near the Desert Tortoise Reserve. In this same vicinity, Busack and Bury (1974) reported that sheep grazing had a negative effect on the lizard populations, probably because of loss of cover, reduction in food sources, disturbances of social structure, and casualties; these factors probably also affect tortoises. Young tortoises have been found crushed by the hooves of livestock. Inferences about the potential and actual impacts of grazing on tortoise populations are further discussed by Berry (1978).

Evidence shows that sheep and cattle grazing have detrimentally affected the Beaver Dam Slope population of desert tortoises in Utah (Woodbury and Hardy 1948; Hardy 1976; Coombs 1977; Berry 1978). Livestock appear to compete with tortoises for many food plants and to cause deterioration of the general condition of the range inhabited by tortoises (by reducing productivity, decreasing available perennials and forbs, and trampling).

Management

Legal Protection

The desert tortoise is legally protected in California; a 1961 statute makes it unlawful to "sell, purchase, needlessly harm, or take the desert tortoise or to shoot any projectile" at it (Leach and Fisk 1969). This statute was further amended in

August 1972 to include prohibition of transportation and possession of all species of *Gopherus* in California (Bury and Stewart 1973). This amendment provides for a permit system whereby owners who can demonstrate legal acquisition may possess tortoises. Permits can also be issued for possession for educational, scientific, and zoological purposes. In 1972, the desert tortoise was declared the state reptile. On 1 March 1972, the California DFG amended its wildlife regulations to include a "zero bag limit" for all species of the genus *Gopherus*. These recent laws prohibit the importation of all North American tortoises (*Gopherus*) into California. The laws are enforced, but manpower is inadequate for proper enforcement. Furthermore, these laws are not widely known. Not only are few tortoise owners aware of their legal obligation to register their pets, some confusion exists as to just how registration should be done and what constitutes a "legal" animal. A solution to these problems is being sought (St. Amant 1977).

Land Ownership

Ownership of lands in the California desert is divided among many agencies and organizations, but Federal ownership predominates. Six military reservations (Edwards Air Force Base, Fort Irwin, U.S. Naval Ordnance Test Station at China Lake, Randsburg Wash Test Range, Twentynine Palms Marine Corps Training Center, Chocolate Mountains Gunnery Range) under the Department of Defense comprise about 1.2 million ha; other agencies in the Department of Interior (National Park Service, Bureau of Reclamation, and the Bureau of Indian Affairs) administer about 0.81 million ha. Private and state ownership account for about 0.45 million ha. The Southern Pacific Land Company is the largest single private owner; its ownership stems from the Public Railway Act of 1862 which granted to the company odd-numbered sections, 32 km on each side of the planned railroad route. Once surveyed, nearly half of the granted lands were sold in the first 20 years to help finance construction, but most of the desert holdings were deemed worthless and remained unsold; Southern Pacific retains ownership and apparently has no immediate plans for development. The State of California is involved with the desert in a variety of capacities, including highway rights-of-way, irrigation districts, school districts, state parks, and fish and game regulation. Private business interests include mines, real estate, agriculture, grazing lands, ranches, and tourist facilities.

Cabins and rural retreats in the form of small tracts (mostly smaller than 2 ha) are the basis for some private ownership patterns in the desert. Between 1959 and 1969, about 20,000 ha were sold under the Federal Small Tract Act for small-acreage recreational homesites; the largest concentration of these lies in the western Mojave Desert from just east of Twentynine Palms to Victorville, with smaller concentrations in the Antelope Valley and in the Barstow and Ridgecrest regions. As a result of these and other land sales of the 1950's and early 1960's, an estimated 120,000 unimproved small parcels are now privately owned in the California Desert. Tortoises are found throughout the low-lying areas in these regions of "jackrabbit homesteads."

Also, mining claims number more than 250,000 (BLM 1969). Mining activities, however, occupy only a small percentage of the land area and most are concentrated in upland areas that are less frequented by tortoises.

The largest portion of the California desert is administered by the BLM, which manages about 4.45 million ha. These lands were primarily designated as grazing and mining leases or held without designated uses. Such lands are now being classified under broader multiple-use designations (BLM 1980), but recreational use and energy development are foremost. Such planning places the future of many tortoise populations in jeopardy because nearly all major concentrations and prime habitat of desert tortoises in California are located on BLM Natural Resource lands.

A major conservation effort is under way to establish a Desert Tortoise Reserve near California City in the western Mojave Desert. This proposed reserve contains the highest known densities of the tortoise. The BLM is attempting to set aside 98 km^2 of land for its natural values, principally for protection of the desert tortoise. A Desert Tortoise Preserve Committee has been instrumental in promoting the reserve (Forgey 1977) and works with its own funds. The Nature Conservancy has also assisted by purchasing a few critical parcels of private land. The proposed reserve has been fenced to deter unauthorized grazing and impact by ORVs, and a nature center and trail system for the reserve are now being considered.

Energy leases and transmission corridor easements on natural resource lands have been granted to various power and utility companies. Some of these projects consider the best possible planning alternatives with respect to tortoise populations (e.g., Stevens 1976). Other projects have opened access to desert lands through road construction along corridor routes for transmission lines or underground pipelines.

The Department of Defense lands in the California desert probably support sizeable tortoise populations (Berry 1976). These facilities have served as reserves because of their restricted use patterns and controlled access. Conversely, some attrition has probably occurred during the various training exercises.

Desert Tortoise Council

In 1975, a Desert Tortoise Council was established through the volunteer efforts of representatives from local, State, and Federal agencies, and from utility companies, colleges, and universities, as well as private citizens and civic groups. Its major aims are to provide a forum for discussion of the problems of tortoise management and to coordinate efforts relating to the survival of the tortoise throughout its range. Among the activities of the Council are efforts to define tortoise respiratory diseases, the release of rehabilitated captive animals into the wild, and several education projects to focus attention on the plight of the tortoise. The Executive Committee of the Council now meets several times each year and annual symposiums are held. Work on the management and biology of the tortoise is published in the *Proceedings of the Desert Tortoise Council.*

Recommendations

My field studies have identified several prime tortoise areas (Table 4); existing reserves for the desert tortoise in California are given in Table 5. Only in the Desert Tortoise Reserve has a substantial tortoise population been identified for protection.

The ancestors of the desert witnessed the large-scale Pleistocene extinctions of many animal species, but they adapted to the increasing aridity of the Southwest. The tortoise survived this period to become the largest native herbivore on most of the Southwestern flatland desert. The desert tortoise is well adapted and resistant to the climatic and biological demands of an arid region, but its future survival is in jeopardy because of human activities. Tortoise populations have already suffered significant losses from collection and removal, grazing, roadkill, military activity, and vandalism, and more recently by rapidly increasing ORV use. Its habitat is extremely vulnerable to disruption by ORVs.

Although the desert tortoise has adequate legal protection in California, its habitat does not. The major high-density areas are largely on BLM-administered public lands. The future of the desert tortoise can best be assured by proper management of these lands for their wildlife values.

Specific management needs of the desert tortoise identified by the present study include the following:

- Prohibit or restrict use of ORV activities in areas of high tortoise abundance;
- Investigate the impacts of grazing, especially the short-term, concentrated trailing of sheep;
- Coordinate efforts of the Department of Defense in California to identify areas critical to unique wildlife and plant species on their lands, and to adopt suitable management programs within the framework of their research and training priorities; and
- Coordinate similar efforts concerning tortoise populations in other states and in northwestern Mexico.

Acknowledgments

I am deeply grateful to R. B. Bury, Denver Wildlife Research Center, for his encouragement and guidance, which was unselfishly extended during all stages of the study. I appreciate the assistance of the World Wildlife Fund, who supported my field work.

Many people have assisted during the course of this study. In particular, I thank K. and R. Berry, R. W. Marlow, R. and K. S. Norris, R. Patterson, R. C. Stebbins, and G. R. Stewart. I am indebted to F. and M. Fairchild of the California State Parks, who first introduced me to the Mojave Desert.

Others who provided important assistance include: J. and K. Cornett (Desert Hot Springs), J. Edell (Bishop), U. Gallinairi (Gold Valley Ranch), M. Getty (Anza Borrego Desert State Park), J. and M. Howard (Essex), L. Hunter (Barstow Unified School District), E. P. Pister (California Department of Fish and Game), D. Powell (University of California at Berkeley), T. Oberlander and J. J. Parsons (University of California at Berkeley), P. Sanchez (Death Valley National Monument), and D. and N. Shade (Twentynine Palms).

Special thanks are due B. and M. Luckenbach for their patience and understanding.

Table 4. *Prime desert tortoise areas in California.*

Locality	Habitat	Human disturbance	Ownership	ORV Classification[a]
1. Upper Ward–Chemehuevi Valleys	Creosote scrub with ocotillos. Cholla gardens and other succulents; wash.	Area of "Desert Strike" maneuvers; unexploded ordnance, some trash, tracks (heavy in NE). N-S power line; E-W Gas and power lines and access roads.	Most bajadas of Ward Valley are consolidated BLM Natural Resource Lands. Most of Chemehuevi Valley is BLM lands, but northern part is mixed ownership.	Valleys: existing roads and trails. Old Womans area and perimeter of Turtle Mtn.: designated roads and trails. Small closure by I-40. North of 40: designated road and trails.
2. Fenner and Piute Valleys	Creosote scrub, cholla gardens, and other succulents; wash.	Area of "Desert Strike" maneuvers: ordnance, fox holes, trash, airport, old barracks; range cattle; roads; power and gaslines.	Mining claims. Railroad checkerboarding, private lands, mining claims, and grazing leases.	Western end of Fenner Valley: existing roads and trails. The remainder: designated roads and trails.
3. Water Valley	Creosote scrub, Joshua Tree woodland.	Power and gaslines; roads; sheep use seasonally; old mines.	Railroad checkerboarding on western end. Some consolidated BLM land on east end. Private lands.	Eastern end: designated roads and trails. Western section: some ORV event design sites.
4. Fremont Valley	Creosote scrub, Joshua Tree woodland.	Subdivisions; powerlines; encroaching irrigated agriculture; numerous roads; sheep grazing seasonally; ORV activity.	Almost wholly in private sector with exception of tortoise preserve.	Unclassified because of private ownership. Tortoise Reserve is closed.
5. Stoddard Valley	Creosote scrub, Mojave yucca, and other succulents at higher elevations.	Power and gas line roads; mining activity in past. Range cattle, sheep grazing seasonally; camping and ORV activity.	Mostly consolidated BLM lands; grazing leases, some patented mining claims.	Special design and existing roads and trails. Competitive Events Areas.
6. Ivanpah Valley	Creosote, shadscale and alkali, sink scrub.	Power and gasline roads; Union Pacific railroad; range cattle.	Largely BLM lands with some school district sections. Some private lands near Cima. Grazing leases.	Designated roads and trails.
7. E. Kramer Hills W. Hinkley Valley	Creosote scrub, scattered Joshua Trees.	Power and gas line roads; subdivisions; and small private tract plots; sheep grazing seasonally; ORV activity.	East of Hwy 395, well-consolidated BLM lands. Mostly private holdings along Mojave flood plain and in Hinkley Valley.	Kramer Hills is a special design area. An ORV Competitive Events Area is planned.

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[a] Refers to classifications in the California Desert ORV Recreation Management Plan (1 November 1973).

Table 5. *Areas serving as reserves for the desert tortoise in California.*

Name	Facility	Size (ha)	Comment
Joshua Tree	National Monument	18,200	Moderate numbers of native and released animals.
Death Valley	National Monument	810,000	Low population densities.
Picacho	State Park	1,975	Status of tortoises, if present, unknown.
Providence Mtns.	State Recreation Area	2,120	Small numbers at lower elevations.
Saddlebag Butte	State Park	1,160	Abundant: frequent release site.
Redrock Canyon	State Park	800	Resident populations severely reduced.
Wildflower and Wildlife Sanctuaries	Los Angeles County Park	860	Eight separate sanctuaries--mostly in creosote scrub in Antelope Valley. Tortoises locally abundant.
Desert Tortoise Reserve	BLM and private land	8,500	Highest known densities in Calif. Education and scientific use area.

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Appendix

Pooled data from 5 surveys conducted on the Desert Tortoise Reserve, 5 on the Hinkley Study Site, 33 from high-density areas, 69 from medium-density regions, and 35 from low-density areas. Total values are averages plus or minus one standard deviation; ranges are given in parentheses—i.e., $\bar{x}$ ± SD (range).

Standardization Transects

Site	Transect	Tortoises		Burrows		Scats
		Adult	Juvenile	Active	Inactive	
Desert Tortoise Reserve (N=5)	A	26	0	40	48	18
	B	8	0	60	36	21
	C	17	0	36	40	16
	D	20	4	46	44	24
	E	43	3	42	38	19
		22.8±13.0 (8-43)	1.4±1.9 (0-4)	44.8±9.2 (36-60)	41.2±4.8 (36-48)	19.6±3.0 (16-24)
Hinkley Study Site (N=5)	A	18	0	36	24	20
	B	9	2	30	19	29
	C	14	0	16	12	12
	D	15	1	26	21	36
	E	16	1	22	18	17
		14.4±3.4 (9-18)	0.8±0.8 (0-2)	26±7.6 (16-36)	18.8±4.4 (12-24)	22.8±9.6 (12-36)

High Density (N=33)

Transect	Tortoises		Burrows		Scats
	Adult	Juvenile	Active	Inactive	
5	0	0	18	22	7
7	4	0	27	31	12
8	7	2	35	26	15
9	6	1	20	33	9
17	5	1	36	24	32
18	6	0	19	27	7
21	2	2	31	35	0
26	8	3	39	26	9
27	0	0	25	19	2
29	1	0	32	29	11
30	10	3	31	36	22
31	3	2	21	28	14
32	6	1	36	27	3
54	3	1	19	24	10
58	6	1	43	31	0
63	4	0	19	26	4
66	2	0	24	32	23
67	3	0	31	41	25
68	8	2	37	29	17
69	4	0	22	30	13
70	0	0	41	34	17
71	2	0	29	19	5
72	7	1	36	26	11
78	6	0	28	17	19
80	0	0	28	18	7
81	9	2	30	27	3

High Density (N=33) continued

Transect	Tortoises		Burrows		Scats
	Adult	Juvenile	Active	Inactive	
82	4	0	27	36	9
91	3	1	39	37	22
94	2	0	29	19	14
96	6	0	37	28	6
97	10	0	47	36	11
98	7	2	39	29	14
101	2	0	40	32	21
	4.4±3.0 (0-10)	0.8±1.0 (0-3)	30.7±7.8 (18-47)	28.3±6.0 (17-37)	11.9±7.7 (0-32)

Medium Density (N=69)

Transect	Tortoises		Burrows		Scats
	Adult	Juvenile	Active	Inactive	
4	2	0	14	7	3
6	7	0	17	10	0
10	0	0	12	14	5
11	5	1	9	7	1
12	6	1	13	13	4
13	1	0	8	21	9
14	3	0	14	6	14
15	6	2	10	3	2
16	2	0	16	11	2
19	1	1	9	6	9
20	9	3	27	13	11
22	0	0	9	3	11
23	8	0	11	7	0
24	0	0	14	5	1
25	5	2	16	0	0
28	2	0	6	3	6
35	11	2	29	14	17
36	4	0	27	19	0
38	6	2	15	7	13
40	7	1	18	9	7
42	4	0	20	11	1
44	0	0	8	3	10
48	2	1	10	7	9
52	1	0	9	4	2
53	2	0	14	9	0
55	0	0	4	1	7
56	9	3	18	17	3
57	3	1	16	2	20
59	2	0	15	7	17
60	4	0	10	8	7

Medium Density (N=69) continued

Transect	Tortoises		Burrows		Scats
	Adult	Juvenile	Active	Inactive	
61	3	0	9	7	9
62	0	0	7	9	15
64	1	0	3	0	4
65	2	1	5	1	3
73	0	1	7	4	9
74	4	0	9	13	3
75	2	0	12	3	8
76	2	2	17	9	0
77	1	0	8	6	2
79	7	1	13	10	12
83	11	0	28	17	13
84	0	0	16	11	17
85	4	0	21	14	7
88	3	1	15	13	9
89	0	0	9	5	3
90	5	3	12	3	2
92	2	1	7	0	2
93	0	1	18	4	7
95	1	0	15	8	0
99	2	0	7	12	11
102	0	0	11	8	3
103	1	0	17	13	10
104	3	2	7	10	7
105	0	0	11	9	5
106	4	1	14	16	12
107	4	0	10	17	5
108	1	2	9	3	2
109	0	0	10	14	3
110	1	0	18	16	2
112	4	0	17	12	2
113	8	4	22	12	7
114	2	3	5	11	0
125	2	1	14	9	7
126	4	2	17	7	11
128	0	0	22	14	3
129	5	1	13	3	0
130	0	2	11	16	2
131	5	1	21	5	9
136	3	0	18	17	0
	3.0±2.8 (0-11)	0.7±1.0 (0-4)	13.2±5.6 (3-29)	8.8±5.1 (0-21)	6.0±5.1 (0-20)

Low Density (N=35)

Transect	Tortoises		Burrows		Scats
	Adult	Juvenile	Active	Inactive	
1	0	0	0	0	0
2	0	0	0	1	0

Low Density (N=35) continued

Transect	Tortoises		Burrows		Scats
	Adult	Juvenile	Active	Inactive	
3	0	0	0	3	0
33	1	0	3	2	0
34	1	0	5	2	0
37	3	1	8	5	0
39	4	0	9	11	7
41	0	0	0	2	0
43	2	0	0	1	3
45	0	0	3	1	0
46	2	1	13	2	2
47	3	1	17	9	7
49	2	0	19	11	5
50	4	0	9	2	1
51	1	0	3	0	0
86	0	0	4	2	0
87	0	0	1	2	0
100	3	1	6	1	7
111	0	0	2	2	0
115	1	0	7	9	2
116	1	0	4	3	0
117	0	0	2	0	0
118	1	0	8	10	4
119	1	1	4	3	0
120	2	0	9	5	0
121	0	0	0	0	0
122	0	0	0	0	0
123	0	0	0	0	0
124	0	0	0	2	0
127	1	1	9	1	0
132	2	0	6	4	1
133	1	0	4	1	0
134	0	0	0	0	0
135	0	0	0	0	0
137	0	0	0	0	0
	1.0±1.2 (0-4)	0.2±0.4 (0-1)	4.6±5.0 (0-19)	2.8±3.3 (0-11)	1.1±2.2 (0-7)

Chelonian Conservation and Biology, 2000, 3(4):714–721

Environmental Characteristics of Desert Tortoise (*Gopherus agassizii*) Burrow Locations in an Altered Industrial Landscape

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ABSTRACT. – **In the Colorado Desert of California, the western distributional limit of the desert tortoise (*Gopherus agassizii*) occurs in the Whitewater Hills of the southeastern San Bernardino Mountains. Much of the area has been developed for wind energy generation and tortoises often live in association with altered industrial landscapes. Natural habitat in the area was characterized by a sharp transition zone of plant associations including representatives of the Colorado and Mojave Deserts, coastal, and montane ecosystems. We examined the environmental factors associated with the locations of desert tortoise burrows at a site developed for wind energy generation. Measurements were taken at the opening of burrows, including elevation, slope, aspect, and distance to various natural and anthropogenic features of the landscape. We compared this data set with identical measurements for random points that lacked burrows in the same landscape. The analysis demonstrated that desert tortoises within the study area did not randomly select their burrow sites. Desert tortoise burrows were located closer to roads and concrete foundations associated with wind energy turbines and transformers than were random points. The results challenge the paradigm that desert tortoises are negatively affected by all forms of anthropogenic disturbance and suggest that with proper planning, some forms of development in the desert are compatible with conservation of sensitive species.**

KEY WORDS. – **Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; burrows; wind energy generation; habitat selection; Mojave Desert; Colorado Desert; California; USA**

Habitat use by animals is influenced by several factors that can have a dramatic influence on an individual's fitness. Selection of specific habitats can facilitate access to important resources such as food, water, mates and brood/nest sites, provide protection from predators and harsh environmental conditions, and limit competition with con- and hetero-specifics. When specific habitats are selected by animals, they are used disproportionately to their availability. Major assumptions of habitat selection are that animals select habitats that maximize their ecological requirements and fitness, and that high quality habitats are selected more than low quality habitats (Rosenzweig, 1981; Manly et al., 1993). In comparison with transient occupancy of habitat, location of nests, burrows, and other structures used by animals for longer periods of time represent a relatively long-term, and potentially costly, commitment to a particular microhabitat (Hansell, 1993). Consequently, the location of these structures has significant physiological and life-history consequences (Fig. 1).

The desert tortoise (*Gopherus agassizii*) is federally protected as a threatened species throughout about half of its range in the United States, which includes portions of California, Nevada, Arizona, and Utah (Fish and Wildlife Service, 1994). In California, as much as 98% of the annual activity cycle of the desert tortoise is spent underground in burrows or other shelter sites that it usually constructs (Nagy and Medica, 1986). Burrows are used for thermoregulation (McGinnis and Voigt, 1971; Zimmerman et al., 1994), hibernation (Bailey et al., 1995; Rautenstrauch et al., 1998), nesting sites (Turner et al., 1986), and as foci for social interactions (Bulova, 1994, 1997). The location of burrows can also provide protection from flooding and fire. Burrows provide a special microhabitat where the humidity is higher and the temperature is lower and more constant than the environment on the surface. Thus, using burrows helps reduce evaporative water loss rates and provides protection from thermal extremes. Under adverse surface conditions, desert tortoises may stay in burrows for weeks or months at a time (Ernst et al., 1994).

Most research on the desert tortoise has focused on areas far removed from human population centers, although much of the habitat occupied by desert tortoises has been affected by humans to some extent (Lovich and Bainbridge, 1999), sometimes severely. Although human activities have been invoked as causes of population declines in the species (Fish and Wildlife Service, 1994; but see Corn, 1994, and Bury and Corn, 1995), few data are available to evaluate these impacts critically. The purpose of this study was to examine the environmental characteristics of desert tortoise burrow locations in an industrial landscape developed for wind energy generation near Palm Springs, California. Two questions were asked at the beginning of the study: (1) do desert tortoises randomly locate burrows in the study area? and, (2) if burrow locations are not random, do desert tortoises avoid constructing burrows in proximity to industrial activities?

METHODS AND MATERIALS

Site Description. — The study site was located on land administered by the Bureau of Land Management (BLM) in the Whitewater Hills of the southeastern San Bernardino Mountains in western Riverside County, California. The area, known locally as the Mesa wind park (Mesa), was developed for wind energy generation starting in the 1980s. Wind energy turbines and their associated infrastructure were the most conspicuous elements of the landscape with about 460 turbines, 51 electrical transformers, and an extensive network of unpaved roads in place at the time of the study (Fig. 2). Concrete foundations were associated with each turbine and electrical transformer. In addition, the area was grazed by cattle in most years as part of the Whitewater Grazing Allotment administered by the BLM. A vigorous breeding population of desert tortoises occupies the site (Lovich et al., 1999).

The study site was characterized by a mixture of plant communities representing several ecosystems. Sitting at the interface between coastally influenced plant associations and the desert, Mesa had exceptional perennial plant diversity. North-facing slopes and the western edge of the study area were dominated by chaparral and coastal sage scrub plant species (Schoenherr, 1992) including chamise (*Adenostoma fasciculatum*) and California sage brush (*Artemisia californica*). Other cismontane species (*sensu* Schoenherr, 1992) included California juniper (*Juniperus californica*), condalia (*Condalia parryi*), and isolated oaks (*Quercus* spp.). South-facing slopes and the eastern edge of the study area were characterized by typical Mojave Desert (Vasek and Barbour, 1977) and Colorado Desert (a subdivision of the Sonoran Desert, Burk, 1977) plants, including creosote bush (*Larrea tridentata*), burrobush (*Ambrosia dumosa*), honey mesquite (*Prosopis* spp.), cholla (*Opuntia* spp.), bladder pod (*Isomeris arborea*), linear-leaved goldenbush (*Haplopappus linearifolius*), encelia (*Encelia farinosa*), and cheesebush (*Hymenoclea salsola*). A signature species of the Colorado Desert that occurred on site was teddy-bear cholla (*Opuntia bigelovii*). Another species, spiny hopsage (*Grayia spinosa*), a common plant of the Mojave Desert, but rare in the Colorado Desert except for the Whitewater Hills (Jaeger, 1940), was relatively abundant. The study site was mountainous with elevations at desert tortoise capture locations ranging from about 660 m in the valleys to over 880 m on the peaks and ridges. The topography at the northern boundary of the study site limited the distribution of tortoises, which usually occur below 1500 m (Germano et al., 1994), as elevation rises sharply to over 3500 m.

Figure 1. The location of a desert tortoise burrow can have dramatic consequences for its occupant. This photograph shows the carcass of a desert tortoise that died of third-degree burns in its burrow during a wildfire at the study site. The shallow burrow was located under a dense thicket of *Grayia spinosa* that ultimately became the funeral pyre for the animal. If the burrow would have been located in the open, or if it had been deeper, the occupant may have survived. Many of the tortoises at the site bear the scars of encounters with fire. Photo by JEL.

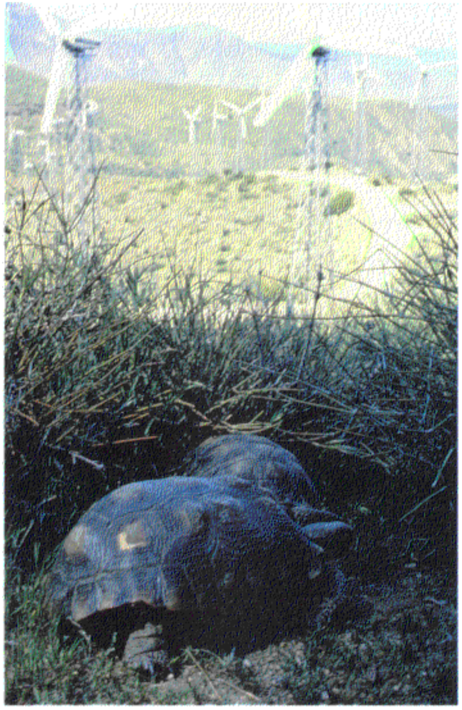

Figure 2. Partial view of study site showing wind energy turbines and desert tortoises (female in foreground, male in background) as they were found. The female bears the remnants of an old tag that was epoxied to her shell by a previous researcher for purposes of individual identification. Photo by JEL.

The study site was at the westernmost edge of the distribution of the desert tortoise in the Colorado Desert (Luckenbach, 1982; Patterson, 1982), where the steep terrain and unique plant associations are atypical of desert tortoise habitat elsewhere in the Colorado Desert (Fish and Wildlife Service, 1994). The coastally influenced climate resulted in greater rainfall than tortoise habitat immediately to the east, due to a rain-shadow effect, and this generally promoted high production of winter annual plants (Lovich et al., 1999) on which desert tortoises feed.

Methodology. — We collected data during 1995 and 1996, although anecdotal observations continued through 1998 during the course of our separate research on the reproductive ecology of desert tortoises at the site (Lovich et al., 1999). Burrows were located during systematic searches

Table 1. Desert tortoise (*Gopherus agassizii*) burrow attributes reported in the literature. Aspect refers to the predominant orientation of the entrance of the burrows.

Aspect	Slope	Cover Association	Region	Reference
North-northeast	—	72% under shrubs	southern Nevada	Burge, 1978
West-southeast	—	79% under shrubs	California deserts	Berry and Turner, 1986
North	—	—	southern Nevada	Bulova, 1994
South	44.1º	40% under shrubs	Arizona	Bailey et al., 1995
—	—	68% under perennial plants	California	Duda, 1998
Southwest	17.7º	41% under shrubs	Mesa, California	This study

of the wind park conducted by walking transects through areas bounded by unpaved roads or rows of turbines. Only burrows that were approximately shell-depth or more (thus excluding shallow excavations or pallets according to the definition of Burge, 1978), and known or appearing to be actively used, were included in the statistical analyses. All burrows but one, occupied by a juvenile, were typical of the size used by adult tortoises (18–37 cm carapace length, Ernst et al., 1994). The following variables were quantified for each burrow: SLOPE (in degrees), ASPECT (compass direction in degrees of the predominant facing slope), and ELEVATION. In addition, distances were measured from the opening of each burrow to various natural and anthropogenic features in the landscape, including the following variables: ROAD (unpaved roads, as no paved roads are located at the site), PAD (concrete foundations for turbines and electrical transformers), LARREA (creosote bush, *Larrea tridentata*), ENCELIA (brittlebush, *Encelia farinosa*), CACTUS (several cactus species of the genus *Opuntia*), YUCCA (*Yucca* spp.), and ROCK (rock outcrops or rockpiles). These variables were selected because they were prominent features of the landscape. Distance variables were measured using a flexible tape. All plants were alive at the time the burrow was constructed, although many were dead at the time of measurement due to the effects of a major fire in 1995. The importance of using fine scale habitat characteristics to infer ecologically meaningful patterns in desert tortoise burrow distribution has previously been demonstrated by Baxter (1988). Computer-generated random points were used to locate sites that did not have burrows and the same variables were measured. The statistical analysis included 32 desert tortoise burrows and 32 random points.

Following Zar (1984), data were transformed for statistical analyses using the natural logarithm of (x+1), unless indicated otherwise, to meet the assumption of normality. Multivariate Analysis of Variance (MANOVA) was used to assess the overall significance of differences between all variables measured (except ASPECT) for burrows and random plots. This technique is superior to using multiple univariate ANOVAs because it uses correlations among characters rather than ignoring them (Willig et al., 1986). Principal components analysis (PCA) was then used on transformed variables, normalized to have a mean of zero and a standard deviation of one, as a data reduction technique to identify orthogonal factors and the variables that loaded highly in each. Separate MANOVAs were calculated for variables that loaded highly in each factor. Following identification of multivariate significance, a two-group discriminant function analysis (DFA) was conducted using the influential variables selected with PCA. The classification accuracy of the function was assessed by tabulating actual locations (burrows and random points) vs. locations predicted by the function.

Because ASPECT is a circular scale variable, it was analyzed separately using Oriana© software for circular statistics. Other statistical procedures were executed using SYSTAT (Wilkinson et al., 1992). Levels of statistical significance were set at an alpha of 0.05.

RESULTS

Of the 32 burrows analyzed, 13 (41%) were located under shrubs, including *Larrea*, *Ambrosia*, *Ephedra* sp., *Hymenoclea*, and *Grayia* (Table 1). One of the burrows included in our statistical analysis was located under the concrete pad of an electrical transformer (Fig. 3a). Subsequent observations made after our study concluded, but not included in our statistical analysis, demonstrated that this was not an unusual burrow location and that burrows were commonly associated with anthropogenic features in the landscape (Figs. 3b-f).

There were few significant differences among the variables measured, with YUCCA being the single exception (Table 2). However, the results of a MANOVA using log-

Table 2. Means, standard deviations (in parentheses), and ranges for variables measured at desert tortoise burrows and random points. The probability for ASPECT is based on Watson's F-test for two circular means. Probabilities for other variables are based on univariate F-tests (ANOVA) comparing the means of log-transformed data for burrows and random points. All measurements are in meters, except for slope and aspect, which are in degrees.

	SLOPE	ASPECT	ROAD	PAD	LARREA	ENCELIA	CACTUS	YUCCA	ROCK	ELEVATION
Burrows	17.7	188.3	22.1	49.7	16.8	5.1	4.8	31.7	10.3	770.3
	(10.2)	(66.5)	(22.6)	(77.1)	(25.4)	(6.0)	(4.6)	(30.1)	(16.0)	(32.3)
	0–45	26–340	0–101	0–343	0–100	0.2–24.4	0–25	3.3–102	1.7–92.4	699.8–844.3
Random	15.9	193.1	33.9	66.2	23.7	6.5	7.8	16.1	14.7	775.1
	(10.7)	(97.3)	(41.5)	(59.2)	(45.4)	(5.9)	(9.7)	(18.4)	(14.1)	(29.0)
	2–40	88–360	0–145.8	0.5–188.8	0–233	0.2–24	0.7–51.1	1–90	1.2–47.7	719.3–850.4
Probability	0.62	0.84	0.96	0.14	0.61	0.21	0.12	0.04	0.18	0.53

Figure 3. Desert tortoise burrows at the study site were frequently associated with human disturbances in the environment. All photos by JEL unless noted otherwise. **(a)** This female, visible in the center of the photograph, constructed her burrow under the concrete pad of an electrical transformer and shared it with a packrat (*Neotoma* spp.). Her frequent use of the burrow (spanning about 2 years) was shown by scratches on her carapace caused by passing under the concrete lip of the foundation. Photo by Claude Kirby. **(b)** Another female used a burrow under a different electrical transformer pad. The entrance is the wide area shown on the right side of the pad. **(c)** Yet another female constructed her burrow in the road cut next to a turbine. She deposited a clutch of eggs in the apron of her burrow in 1997. **(d)** Close-up of a juvenile desert tortoise (6.9 cm carapace length) at the entrance to the burrow shown in Fig. 3e. **(e)** A juvenile desert tortoise constructed a burrow under a piece of waste concrete next to a turbine. A lens cap (lower center of the photograph) is shown above the entrance to the burrow. **(f)** Desert tortoise burrows at the study site are frequently constructed in cut banks along roads. Note the burrow under the white marker pole.

transformed data for all variables except ASPECT, revealed significant differences among the variables characterizing burrows and random points (Wilk's Lambda = 0.730; df = 9, 54; $p = 0.035$). The mean vector for burrow ASPECT was southerly (188.3º) but it was not significantly different from the mean vector (193.1º) for random points (Watson's F-test, F = 0.04, $p = 0.84$, df = 62; Table 2, Fig. 4).

PCA revealed four principal components with eigenvalues greater than unity that together explained 74.7% of the total variance. The first principal component was related to anthropogenic features in the landscape as shown by high loadings for ROAD and PAD. The other principal components were related to distance to various plant species (Table 3). A simplified MANOVA using the highest loading vari-

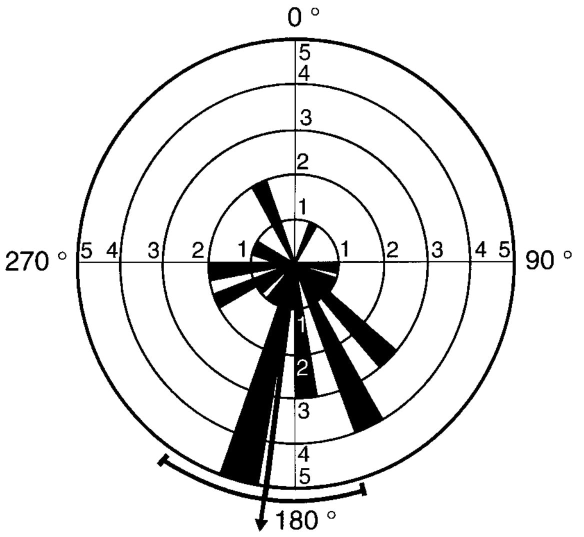

Figure 4. Plot of vectors showing aspect of slopes for locations with desert tortoise burrows. Bar width is 10º. Frequency is shown by the radius of wedge. The mean vector (188.3º) and the 95% confidence interval are shown.

ables in each principal component (PAD, LARREA, YUCCA, ENCELIA) was not significant (Wilk's Lambda = 0.870; df = 4, 59; *p* = 0.080). Because the first principal component was related to anthropogenic features, it seemed logical to include ROAD as another variable in MANOVA. Although ROAD and PAD were correlated as shown by their high loadings and same sign (Table 3), there were many occasions when the nearest road to a burrow or random point was not the road next to the nearest pad (which always had service road access). MANOVA using an expanded model including ROAD, PAD, LARREA, YUCCA, and ENCELIA approached significance (Wilk's Lambda = 0.839; df = 5, 58; *p* = 0.064).

The DFA on PAD, LARREA, YUCCA, and ENCELIA achieved an overall classification accuracy of 67.2% with most misclassifications occurring for burrows (Table 4). An expanded model including ROAD did not change the results appreciably, but a full model incorporating all variables, with the exception of ASPECT, achieved 71.9% classification accuracy (Table 5). The discriminant scores for burrows were significantly different than those for random points as shown by a two-tailed Student's t-test (t = -4.788, df = 62, $p < 0.001$). A summary of habitat relationships based on discriminant scores is depicted in Fig. 5.

Table 3. Unrotated principal component loadings for principal components with eigenvalues greater than one. Variance explained by each component is shown in parentheses.

	Principal Component			
Variable	I (30.717)	II (18.619)	III (13.354)	IV (12.106)
PAD	0.844	0.058	-0.280	0.011
ROAD	0.799	-0.336	-0.116	-0.008
ELEVATION	-0.724	-0.505	0.011	0.087
SLOPE	0.565	-0.449	0.443	0.108
LARREA	-0.476	-0.610	-0.043	0.452
CACTUS	-0.281	0.592	0.146	0.521
YUCCA	0.304	0.262	0.785	0.282
ENCELIA	0.244	0.272	-0.523	0.611
ROCK	-0.334	0.487	0.013	-0.377

DISCUSSION

The results of our analysis demonstrate that desert tortoise burrow sites were not randomly located as shown by the results of MANOVA of log-transformed variables. This was not unexpected in that other investigators have demonstrated the preference of desert tortoises for certain environmental attributes. Baxter (1988) studied desert tortoise burrow locations near Twentynine Palms, California, approximately 50 km from our study site. He found that at the landscape level, burrow distribution was not statistically different from random. However, the abundance of burrows differed across six plant assemblages reflecting both the non-randomness of the plant assemblages in the landscape, and the preference of desert tortoises for certain assemblages, particularly along ecotones. At the same site (near Twentynine Palms), Duda (1998) found that tortoise burrow locations were statistically different from both random and Poisson distributions, with the data further suggesting that the underlying distributions were clumped.

Hibernation burrows of desert tortoises in the Sonoran Desert of Arizona are often associated with vegetation (dead or alive) and packrat (*Neotoma albigula*) nests (Bailey et al., 1995). Most hibernation burrows examined were located on steep (>45º) south-facing slopes in soils composed of silt, silt with loose gravel, diatomite and/or diatomaceous marl, or layers of well-lithified volcanic ash.

The characteristics of desert tortoise burrow sites in southern Nevada were studied by Burge (1978). Most burrows faced east, northeast, or north, and 72% were located under shrubs. Shrubs were utilized disproportionately to their abundance. For example, 37.7% of the burrows located under shrubs were found under *Acacia greggii* despite the low density of that shrub at the study site. According to Burge, the shade provided by *A. greggii* may have been the reason for its disproportionate use. Similarly, burrows were

Table 4. Classification accuracy of discriminant function analysis for variables PAD, LARREA, ENCELIA, and YUCCA. Row totals are in parentheses.

	Predicted Group		
Actual Group	Burrows	Random Points	Total
Burrows	20 (62.5%)	12 (37.5%)	32
Random points	9 (28.1%)	23 (71.9%)	32
Total	29	35	64

Table 5. Classification accuracy of discriminant function analysis for variables ROAD, PAD, LARREA, ENCELIA, YUCCA, SLOPE, CACTUS, ROCK, and ELEV. Row totals are in parentheses.

	Predicted Group		
Actual Group	Burrows	Random Points	Total
Burrows	22 (68.8%)	10 (31.2%)	32
Random points	8 (25.0%)	24 (75.0%)	32
Total	30	34	64

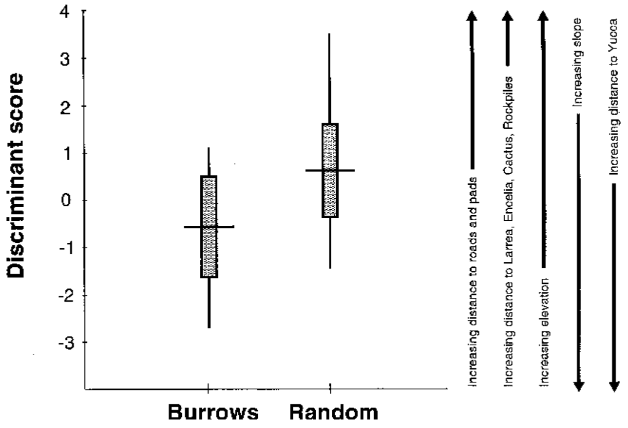

Figure 5. Plot of discriminant score statistics based on a full model incorporating log-transformed ROAD, PAD, LARREA, ENCELIA, YUCCA, SLOPE, CACTUS, ROCK, and ELEV. Means are shown with one standard deviation and ranges for burrows and random points. Arrows show direction of correlation among variables and discriminant scores. The means are significantly different at $p < 0.001$.

frequently located under *Yucca schidigera*, although this plant was numerically under-represented at the study site. Burge suggested that *Yucca* provided roof structure and possibly insulation for burrows. In sharp contrast, the results for our study showed that tortoise burrows were located farther from *Yucca* than were random points, a phenomenon for which we have no explanation.

More recently, Wilson et al. (1999) quantified the physical and microhabitat characteristics of burrows used by juvenile desert tortoises in a field enclosure located in the western Mojave Desert of California. The majority of burrows were located well under large shrub canopies, especially the two species *Larrea tridentata* and *Lycium pallidum*, than were located under the canopy margin or in the open. The mean angle of burrow orientation was 71°. The authors hypothesized that placement of burrows well under large shrubs conferred better protection from predators and/or provided more favorable microclimates for juvenile desert tortoises than burrows located under smaller shrubs or in the open.

Our analysis shows that the principal component explaining the greatest variance in burrow site attributes at Mesa was related to the proximity of anthropogenic features in the landscape. The question that needs to be addressed is: what factors encouraged adult desert tortoises at our study site to locate their burrows in close proximity to roads and turbines? This question is especially pertinent in recognition of well-established evidence showing that roads have generally negative consequences for wildlife due to: (1) mortality of animals along roadways (Rosen and Lowe, 1994; Boarman and Sazaki, 1996), (2) habitat fragmentation and restriction of movements and gene flow, and (3) increased access to remote areas for illegal collection and vandalism of plants and animals (Boarman and Sazaki, 1996). However, none of the roads at our study site are paved and the combination of light traffic (public access is strongly restricted) and generally slow vehicle speeds minimize direct mortality.

Desert tortoises may construct burrows along the elevated berms of unpaved roads because the topography mimics that formed along the banks of desert washes, a preferred site for burrow construction (Luckenbach, 1982). Of the 207 burrows observed by Burge (1978) in large washes, 151 were located in banks with the remainder in the channel bed. She also noted that the elevated dirt berms along roads served as burrow sites for a small portion of her sample. Because desert tortoises appear to prefer the steeply eroded banks of washes for burrow sites in some areas, they may not discriminate between natural banks and the elevated berms associated with most unpaved roads in the desert.

Another explanation for why tortoise burrows at Mesa tend to be located closer to roads than are random points stems from the fact that plant productivity in the desert is often greater along roadsides. “Edge-enhancement” of perennial shrubs along the margin of roads is substantiated by past research in the Mojave Desert showing that plants along roadsides are denser, larger, more vigorous, and support greater numbers of foliage arthropods than those away from roadsides (Vasek et al., 1975; Lightfoot and Whitford, 1991). Primary productivity, as measured by standing crop, increased about 17 times on the basis of vegetated area alone, and 6 times when the area of the bare, paved road surface was included as part of the calculated area. Unpaved roads showed increases of 6 and 3 times, respectively, in each category (Johnson et al., 1975). The increase in vigor has been shown to attract herbivorous insects (Lightfoot and Whitford, 1991), so it is conceivable that the herbivorous desert tortoise selects burrows in close proximity to high densities of food plants as well. In Florida, gopher tortoise (*Gopherus polyphemus*) densities are positively correlated with the percent herbaceous cover, an indicator of food resources (Breininger et al., 1994).

Baxter (1988) found that high density plant ecotones were important determinants of desert tortoise abundance near Twentynine Palms, California, an area that is relatively close to our study site. The distribution of burrows observed by Baxter led him to conclude that desert tortoises are “edge” species. Again, desert tortoises may not discriminate between natural edges and those formed by roads. Similarly, Garner and Landers (1981) observed that roadsides and the edges of fields were common burrowing sites for *G. polyphemus* in Georgia. They also noted that vegetation in those areas generally contained more minerals than food plants on natural sand ridges.

Terrestrial desert chelonians sometimes include roads in their movement patterns. Nieuwolt (1996) observed that some individuals of *Terrapene ornata luteola* used roads to make most of their movements and that distances moved on roads were significantly greater than distances moved off-road. No explanation was offered for the observed difference but it seems logical that roads offer less impediments to terrestrial turtle movement than natural areas and thus facilitate faster transit rates. Desert tortoises sometime use washes and trails as “natural highways” according to Baxter (1988), and it is conceivable that unpaved roads would be used in a similar fashion.

While the scenario above might explain why desert tortoises construct their burrows next to roads it does not necessarily explain why so many locate their burrows under concrete pads. Desert tortoises often construct their burrows under caliche overhangs exposed in the banks of washes (Germano et al., 1994). Caliche overhangs are "hardpan" soil horizons of calcium carbonate crust that form in some desert areas. These layers cement the gravels and cobbles in the soil together, forming a matrix almost as hard as concrete. According to maps presented in a soil survey of Mesa (Soil Conservation Service, 1980), the Chuckwalla Series of soil is noncalcareous throughout and caliche layers do not occur at the locale. Desert tortoises at Mesa may take advantage of the concrete electrical transformer pads as a kind of "artificial caliche," and benefit from the roof stability that they confer. Alternatively, tortoises may associate with concrete because of its thermal inertia relative to soil. On several occasions we have observed desert tortoises "basking" on the pads on overcast mornings when the concrete was notably warmer to the touch than the surrounding soil surface.

The non-random distribution of burrows at Mesa demonstrates the importance of fine-scale habitat characteristics in modeling desert tortoise burrow locations. Some of the unexplained variation in our DFA is probably due to the fact that one tortoise may use more than one burrow over a short period of time. Burge (1978) observed tortoises using 12–25 cover sites per year, and Bulova (1994) found that desert tortoises in southern Nevada used 3–18 burrows during a five month study. At nearby Twentynine Palms, California, Duda et al. (1999) determined that the average number of burrows used per year ranged from 3.1–6.9, and differed among drought and wet years. Better models might be generated by considering individual variation in burrow use. Another source of unexplained variation may be the importance of larger-scale landscape features, as has been demonstrated for *G. polyphemus* burrow orientation by McCoy et al. (1993).

By now it is nearly axiomatic among conservation biologists working in the Mojave Desert that virtually any human alteration of habitat is deleterious to desert tortoise populations (Fish and Wildlife Service, 1994). The cumulative impacts of human activities on ecological patterns and processes in the California deserts are well documented (Lovich and Bainbridge, 1999), but still poorly understood in terms of the exact consequences to wildlife and the habitat on which they depend. While few would argue that outright habitat destruction is anathema to conservation of virtually all wild species, insufficient credible data are available to test the hypothesis that other forms of habitat alteration, or human presence, contributed to the purported decline of the desert tortoise.

While the potentially harmonious situation between desert tortoises and turbines at Mesa is more a result of serendipity than design, the results of our study suggest that certain forms of development may be compatible with conservation of species such as the desert tortoise. Our analysis suggests that the desert tortoise is more adaptable to certain anthropogenic changes in the environment than the above axiom suggests.

Most of the wind energy operations in the area prohibit or greatly restrict access by the public with locked gates, no trespassing signs, and barbed wire fences. This eliminates or greatly minimizes negative impacts associated with vandalism, illegal collection of plants and animals, off-highway vehicle use, and other human impacts (Fish and Wildlife Service, 1994; Brooks, 1999; Lovich and Bainbridge, 1999). In effect, the areas become preserves if they are large enough to meet the needs of the species living therein.

It is important to note that neutral or positive effects of wind energy development to charismatic or politically important species may not be shared by other species or their habitat. For example, wind energy development may cause increased avian mortality (Byrne, 1983; Musters et al., 1996) and increased erosion in hilly terrain (Wilshire and Prose, 1987). Therefore, we are not advocating the proliferation of wind energy development in habitats occupied by either the desert tortoise or other protected species, but rather suggest that by recognizing and planning for the needs of wildlife, the negative impacts of development can be lessened or perhaps even ameliorated.

ACKNOWLEDGMENTS

Alix Marcoux, Robert Lovich, Eileen Kirsch, and Claude Kirby assisted with data collection and other aspects of field work and we appreciate their support. Special thanks to Rowland Griese and the employees of Zond Systems, Inc., for their assistance and cooperation during all phases of the project. Earlier versions of this manuscript benefited from comments offered by Bill Boarman, David Germano, Kathie Meyer, Norm Scott, and Gavin Wright. This paper is dedicated to the memory of Gayle Gronendahl who introduced the senior author to the desert tortoises of Mesa.

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Received: 9 March 1999
Reviewed: 16 May 2000
Revised and Accepted: 5 June 2000

HYUNDAI MOTOR AMERICA MOJAVE PROVING GROUNDS DESERT TORTOISE TRANSLOCATION STUDY

2006 ANNUAL SUMMARY

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March 2007

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BACKGROUND

The Habitat Conservation Plan (HCP) for the Hyundai Motor America (Hyundai) Mojave Proving Grounds Project (Project)[1] detailed the methods and requirements for a translocation program on desert tortoises (*Gopherus agassizii*) removed from the Hyundai Project site[2]. The program included both translocation of tortoises from the Hyundai Project site and a follow-up study on specific effects of translocation.

The primary goals of translocating tortoises from the Hyundai site were to prevent the mortality of tortoises that lived on the site, to maintain the integrity of the population as much as possible, and to maintain breeding individuals in the population. Secondarily, it was hoped that translocation would facilitate the repopulation of another nearby area that had experienced tortoise density declines resulting from drought and disease, and were thereby well under carrying capacity in a normal forage year.

The primary objectives of the translocation study were to address four primary questions:

1 – What is the effect of translocation on survival?
2 – What is the effect of translocation on health status, especially (a) exposure to *Mycoplasma. agassizii* and other pathogens, (b) disease expression, and (c) condition indices?
3 – Is fencing a translocation site a reasonable procedure for site repatriation of areas that are depauperate due to stochastic climatic events or other factors that have not reduced the habitat quality at the translocation site?
4 – How are activity levels affected by translocation?

Each question was further segregated into effects relating to gender, age/size, variation in forage levels, rehydration, activity levels, and time since translocation.

Desert tortoises were removed from the proving grounds and translocated to one of two translocation sites in April of 2004 and 2005 (see attached summaries for the details of each translocation effort). The sites were fenced with tortoise-proof fencing that would removed after at least 18 months to investigate the repatriation objective

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[1] Sapphos Environmental, Inc. 2004. Environmental Assessment/Habitat Conservation Plan for issuance of an engangered species Section 10(A)1(B) Permit for the incidental take of the desert tortoise (*Gopherus agassizii*). January 6, 2004.

[2] Karl, A. E. 2003. Hyundai Motor America Mojave Test Track Site. Desert tortoise translocation program. Appendix A of Sapphos Environmental, Inc,. 2004, Environmental Assessment/Habitat Conservation Plan for issuance of an endangered species Section 10(A)1(B) Permit for the incidental take of the desert tortoise (*Gopherus agassizii*).

of the project. Studies began on the translocated tortoises prior to their translocation, in October 2003, and have been continuous since.

This report summarizes activities in 2006. Data analyses are preliminary and ultimately will be incorporated into comprehensive analyses for each subject area. Such analyses are continually underway for several of the multi-year activities and will become available as results reach a logical threshold.

SITE DESCRIPTION

Based on requirements of the HCP, two translocation sites were established. Site choice was based on habitat quality, carrying capacity considerations, size and proximity to other protected (or likely to be protected) lands, proximity to the Hyundai Project site (i.e., same tortoise population), and ability to protect the site in perpetuity. (See Karl [2003][1] for discussions of these considerations).

The two translocation sites are approximately 30 km northeast of the Hyundai Proving Grounds and adjacent to previously existing lands in the California Department of Fish and Game Ecological Reserve (CDFG ER; Figure 1). They have subsequently become part of that reserve as part of Hyundai Project compensation. The translocation sites are also adjacent to the expansion boundary of another neighboring reserve, the Desert Tortoise Research Natural Area (DTRNA), and the Fremont-Kramer Desert Wildlife Management Area (DWMA).

The westernmost translocation site ("Translocation S12") is one square mile and occupies Section 12 in Township 31S and Range 39E. The eastern translocation site ("Translocation SE") is 1.25 square miles and encompasses Section 17 and the southeastern quarter of Section 18 in Township 31S and Range 40E. Both sites were fenced with wire mesh field fencing prior to translocating tortoises there, in order to preclude entry by sheep and recreationists. Three-foot-wide, tortoise-proof hardware cloth was attached to the lower portion of the fence, with two feet extending above the ground surface and the remaining foot buried, to temporarily keep translocated tortoises in the translocation site.

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The sites have inherently medium quality habitat, based on shrub and annual species present, vegetation density, topography, soils, and substrates. The shrub community is dominated by creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and goldenhead (*Acamptopappus sphaerocephalus*), and snake head (*Ericameria cooperi*), with subdominant cheesebush (*Ambrosia salsola*), winterfat (*Krachenninnikovia lanata*), Mojave aster (*Xylorhiza tortifolia*), stipa (*Stipa speciosa*), and wolfberry (*Lycium cooperi*). The topography is flat to very gently undulating and soils are soft loamy sands. Sheep grazing during the historic past has decreased the habitat quality somewhat by reducing the diversity of shrubs and potentially promoting the dominance of two exotic annuals, split grass (*Schismus

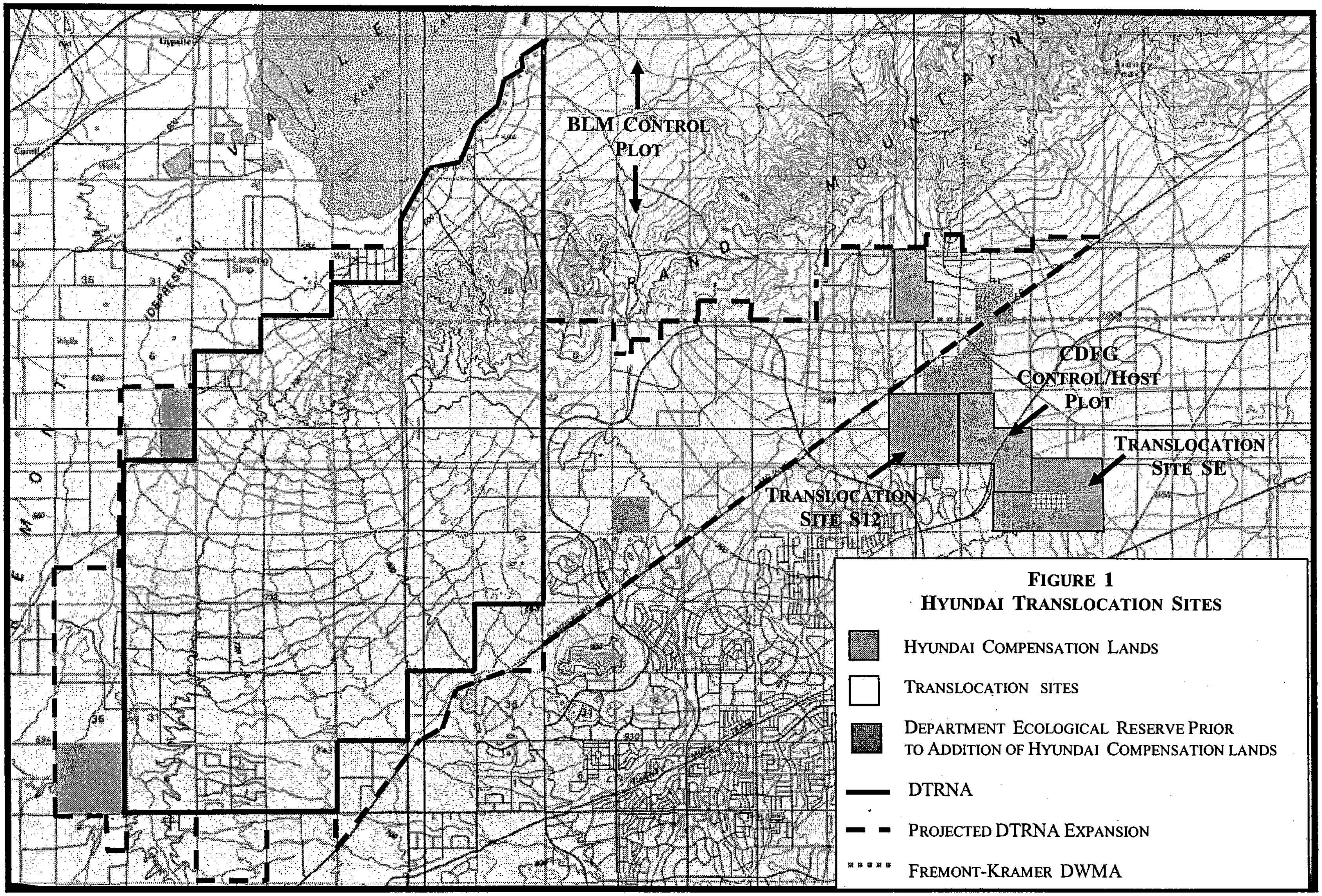

FIGURE 1
HYUNDAI TRANSLOCATION SITES

arabicus) and filaree (*Erodium cicutarium*). There are, however, a number of native species present that are consumed by tortoises (in addition to consuming the split grass and filaree). Onsite disturbances consist of a few well-developed off-highway-vehicle (OHV) trails (motorcycle and all-terrain vehicle) and scattered tracks and faint trails. There are no OHV "play" areas of concentrated damage, although there are a couple of old sheep bedding areas on Translocation SE.

METHODS

Study Cohorts

Hyundai tortoises were translocated to the two translocated sites in April 2004 (Translocation S12) and April 2005 (Translocation SE), because of staggered site availability. (One tortoises, H15, was left outside the Hyundai Project site because she was seropositive for exposure to *Mycoplasma agassizii*.) Both sites were searched for host tortoises prior to releasing translocated tortoises there. However, host tortoises were only found on Translocation SE; none was found in Translocation S12. In March and April 2004, a control site ("BLM Control") was established north of the Rand Mountains (Figure 1) and the site was searched for resident tortoises. A secondary area abutting and between the two translocation sites, and affected both by the initial tortoise-proof fencing as well as the ultimate influx of new tortoises following removal of that fencing ("CDFG Control/Host"), was also searched for resident tortoises. In March and April 2005, the Translocation SE site was searched for host tortoises prior to translocating the remaining Hyundai tortoises there. In summary, the study cohorts consist of:

- ◊ Two translocation cohorts:
    - Translocation S12 - 15 tortoises
    - Translocation SE - 12 tortoises
- ◊ Translocation SE Host Tortoises- 9 tortoises
- ◊ CDFG Control/Host Tortoises - 6 tortoises
- ◊ BLM Control Tortoises - 22 tortoises
- ◊ Hyundai Site (Outside Fence) Tortoises – 1 tortoise

Table 1 describes the size and gender composition of each cohort.

General Methods

At the time of capture, all study tortoises (translocatees, host, and control tortoises) were weighed, measured, photographed, sexed, and described. To facilitate future identification, each was permanently marked (notched) with a unique number, including a distinctive notch to distinguish these tortoises from those used in other nearby studies (e.g., DTRNA trend plots), and secondarily marked with a small epoxy

Table 1
Hyundai Desert Tortoise Translocation Project
Initial Composition of All Study Cohorts, by Site

Translocated Tortoises-Translocation S12

Tortoise Number	Gender	MCL[1]
H 04	Male	299.5
H 07	Male	272
H 08	Female	280
H 14	Male	313.5
H 16	Female	241
H 18	Male	286
H 21	Female	244
H 23	Female	254
H 24	Female	243
H 25	Female	251
H 26	Female	227
H 28	Male	288
H 31	Female	248
H 34	Male	261
H120	Male	267

Translocated Tortoises-Translocation SE

Tortoise Number	Gender	MCL[1]
H 05	Male	282
H 06	Male	299
H 17	Female	260
H 19	Female	247
H 22	Female	255*
H 27	Female	276
H 29	Male	277
H 32	Male	234
H 35	Male	285
H 36	Male	278
H 37	Female	239
H 40	Female	290

Hyundai Site (Outside Fence)

Tortoise Number	Gender	MCL[1]
H 15	Female	248

BLM Control

Tortoise Number	Gender	MCL[1]
H 101	Female	235
H 102	Female	222
H 103	Male	299
H 104	Male	217
H 105	Male	180
H 106	Female	243.5
H 107	Female	238
H 108	Male	263.5
H 109	Female	244
H 110	Male	184.5
H 111	Female	249
H 112	Male	283
H 113	Female	198
H 114	Male	290
H 115	Female	221
H 116	Male	258
H 117	Male	251
H 118	Male	268
H 119	Male	264
H 121	Male	273
H 130	Female	241.5
H 407	Male	230

CDFG Control/Host

Tortoise Number	Gender	MCL[1]
H 201	Male	246
H 202	Male	285
H 203	Male	296
H 204	Female	255
H 205	Male	254+
H 212[2]	Male	209

Translocation SE Host

Tortoise Number	Gender	MCL[1]
H 206	Female	259
H 207	Male	277
H 209	Male	297
H 210	Female	235
H 211	Female	247
H 213	Male	256
H 214	Female	245
H 215	Female	224
H 217	Male	303

1. Maximum Carapace Length at initial capture
2. H212 moved several kilometers away from the study site, so was removed from the Study cohort.

number on the fourth costal. Holohil R1-2B transmitters (24mm wide by 11 mm thick; 14.9 g) were attached to each tortoise, fitted to insure safety to the individual and lack of interference with growth and behaviors (Figure 2). Transmitters are scheduled to last 18or 24 months and are changed prior to scheduled battery life or sooner, if they exhibit symptoms of malfunctioning.

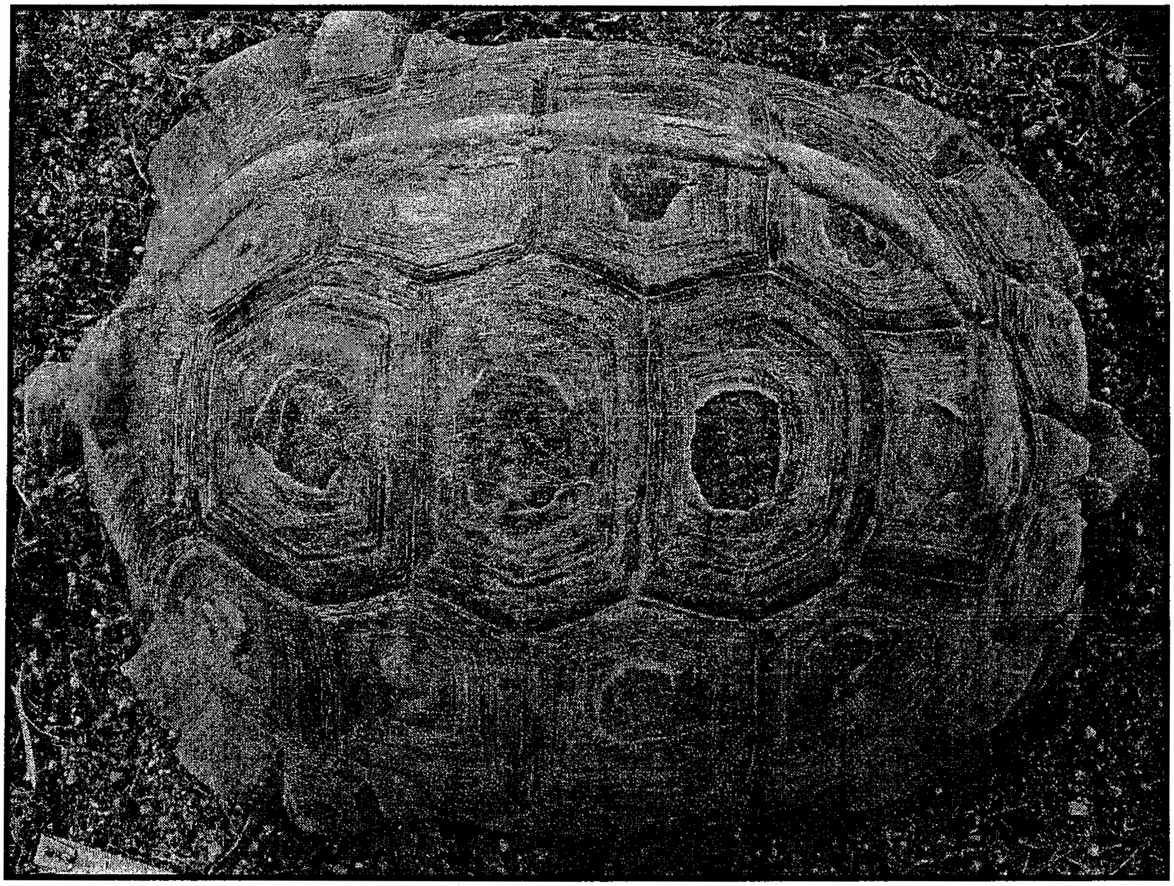

Figure 2. Standard transmitter placement on male Hyundai study tortoises (here, H203). Note the data logger attached to the pygal scute on the left side of the photo.

Survival and general health are monitored through body condition indices (mass to volume ratios[3]), clinical signs, serology and cultures. Condition indices are measured three times during each year: (1) when tortoises exit from hibernation (late March),; (2) following the

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[3] Volume is calculated as half the volume of a spheroid, or ½(4/3·π·r^3). For a tortoise, this translates into ½ [4/3·π·(length/2)·(width/2)·height].

spring activity period and after nesting (July); and (3) immediately prior to hibernation (late October). All tortoises are examined for clinical signs of disease while measuring condition indices. Serum and nasal samples were taken for all study animals at initial capture and at translocation, and are collected annually to test for the presence of antibodies to *Mycoplasma agassizii* (ELISA test) or *M. agassizii* infection (PCR culture), respectively.

Activity patterns (i.e. increased aboveground activity levels), which may affect body temperatures and body condition and ultimately health and survival, are monitored by temperature data loggers (HOBO© TidBits [(www.onsetcomp.com)]), which continuously collect data, every ten minutes. These have been mounted on all males in the study cohorts and also in sample burrows. (Only males can carry the data loggers without interference with righting or copulatory behaviors because the data loggers' tall profile necessitates that the unit be attached to the pygal scute. See Figure 2.)

Translocated tortoises are located on a sufficiently intense schedule to collect the necessary health data, download data loggers, change transmitters, identify faulty transmitters and other equipment, and monitor coarse-grained use areas. In general, this includes locations every ten days during the height of the spring activity period (April), twice-monthly locations during the remainder of the spring activity period (May through June) and fall activity period (October), and once a month in all other months. The exception to this schedule was immediately following translocation. All tortoises were watched for at least one full day immediately following release to observe behaviors and insure that no tortoise exhibited behavior that could compromise survival.

Vegetation data have been collected annually for comparison among all sites, including the original capture site (Hyundai Proving Grounds). Comparisons include plant community characterization (density, frequency, species composition, and percent cover) as well as forage cover and biomass. Specific methods will be presented during a separate report on vegetation results.

Weather is monitored continuously using an HOBO© Weather Station (www.onsetcomp.com) on the Translocation S12 site. Precipitation, wind speed, relative humidity, air temperature, surface temperature, and barometric pressure are recorded hourly. A rain gauge is also maintained on the Hyundai Project site to record precipitation there.

Year 2006

In July 2005, the tortoise-proof fabric at the Translocation S12 site was removed. Because of the possibility of extreme tortoise movements after release, especially following the July 2005 monsoons, translocated tortoises in the Translocation S12 cohort were located three times a week until early September, at which point there was some confidence that they would not be lost due to extreme movements. (Control tortoises were located weekly for comparability of movement.) Rates of locating tortoises remained elevated over normal autumn rates until hibernation, but only at approximately every ten days rather than three times a week.

RESULTS FOR YEAR 2006

Survival

No tortoises died in 2006. To date, only two tortoises in the study group have died, Translocated Male H120 and Host SE Female H215. There was no obvious cause of death for Tortoise H120, who was a relatively old male, judging from shell wear. The female, who died approximately June 1, 2005, apparently died of exposure due to being overturned on a hard surface, where she was unable to right herself prior to overheating.

Health Analyses

Laboratory Results. Titer levels of antibodies identify exposure to *M. agassizii*. No tortoises translocated from Hyundai have seroconverted (i.e., became positive for exposure to *M. agassizii*). Four tortoises have changed titers over the study period: BLM Control tortoises H106, H112 and H119, and the tortoise remaining outside the Proving Grounds, H15. H106 had a titer level of <32 and considered negative for exposure to *M. agassizii* at capture in April of 2004[4]. In April of 2005, this tortoise had a titer level of 32 and was suspect for exposure. In July 2006, the titer was once again <32. H112 had a titer level of 128 at capture in April 2004. In 2005, the titer level was 64 and the tortoise was still considered positive for exposure to *M. agassizii*. In July 2006, the titer level was 32 and the tortoise was considered suspect for exposure. Tortoise H119 was consistently negative through two samplings (April and October) in 2004, with a titer level of <32. In July 2005 and in subsequent samples, the titer level was 32, suggesting a possible exposure to *M. agassizii*.

Tortoise H15, a female from the Hyundai Project site that moved outside the fence prior to the translocation effort and has been monitored as a study animal where she remains, has been continually seropositive since her capture in October 2003. Her titer was 128 from 2003 through 2005. In 2006, the level was 64. Clinical signs have been variable on this tortoise but generally have been confined to swollen eyelids, especially the palpebral. She has never exhibited a nasal discharge or other secretions that are consistent with mycoplasmosis, Other inconsistent signs that may be considered clinical indicators of mycoplasmosis have included occasionally moist nares, moist eyes, or dirt in the nares. However, these conditions are not uncommonly observed in seronegative tortoises and are most likely a response to living in a subterranean, dirt burrow.

Cultures have been consistently negative for all tortoises, even those with positive or suspect titer levels. This is not considered unusual because of the difficulties of culturing the microorganism (Lori Wendland, DVM, University of Florida Mycoplasma lab, pers. comm.).

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[4] The University of Florida Mycoplasma lab rates tortoises as positive, suspect, or negative for exposure, based on titer levels. A titer of 32 is the threshold.

Table 2
Hyundai Desert Tortoise Translocation Project
Comparative Laboratory Results for *Mycoplasma agassizii* Exposure and/or Infection From Initial Capture and Year 2006

Tortoise	Condition at Initial Capture			Condition in 2006		
	Titer	ELISA Result	PCR Result	Titer	ELISA Result	PCR Result[1]
Translocated Tortoises-Translocation S12						
H 04	<32	Negative	Negative	<32	Negative[2]	Negative
H 07	<32	Negative	Negative	<32	Negative	Negative
H 08	<32	Negative	Negative	<32	Negative	---[1]
H 14	<32	Negative	Negative	<32	Negative	---[1]
H 16	<32	Negative	Negative	<32	Negative	---[1]
H 18	<32	Negative	Negative	<32	Negative	Negative
H 21	<32	Negative	Negative	<32	Negative	---[1]
H 23	<32	Negative	Negative	<32	Negative	---[1]
H 24	<32	Negative	Negative	<32	Negative[2]	---[1]
H 25	<32	Negative	Negative	<32	Negative[2]	---[1]
H 26	<32	Negative	Negative	<32	Negative	---[1]
H 28	<32	Negative	Negative	<32	Negative[2]	Negative
H 31	<32	Negative	Negative	<32	Negative	Negative
H 34	<32	Negative	Negative	<32	Negative	Negative
H 120	<32	Negative	Negative	<32	Negative[3]	Negative
Translocated Tortoises-Translocation SE						
H 05	<32	Negative	Negative	<32	Negative	---[1]
H 06	<32	Negative	Negative	<32	Negative	Negative
H 17	<32	Negative	Negative	<32	Negative	---[1]
H 19	<32	Negative	Negative	<32	Negative	Negative
H 22	<32	Negative	Negative	<32	Negative	Negative
H 27	<32	Negative	Negative	<32	Negative	---[1]
H 29	<32	Negative	Negative	<32	Negative	Negative
H 32	<32	Negative	Negative	<32	Negative	Negative
H 35	<32	Negative	Negative	---[5]	---[5]	---[1]
H 36	<32	Negative	Negative	<32	Negative	Negative
H 37	<32	Negative	Negative	<32	Negative	---[1]
H 40	<32	Negative	Negative	<32	Negative	---[1]
Translocation SE Host						
H 206	<32	Negative	Negative	<32	Negative	Negative
H 207	<32	Negative	Negative	<32	Negative	Negative
H 209	<32	Negative	Negative	<32	Negative	Negative
H 210	<32	Negative	Negative	<32	Negative	Negative
H 211	<32	Negative	Negative	<32	Negative	Negative
H 213	<32	Negative	Negative	<32	Negative	Negative
H 214	<32	Negative	Negative	<32	Negative	Negative
H 215	<32	Negative	Negative	<32	Negative[3]	Negative

H 217	<32	Negative	--- (1)	<32	Negative	--- [1]
BLM Control						
H 101	<32	Negative	Negative	Tortoise is temporarily lost		
H 102	<32	Negative	Negative	<32	Negative	Negative
H 103	<32	Negative	Negative	<32	Negative	Negative
H 104	<32	Negative	Negative	<32	Negative	Negative
H 105	<32	Negative	Negative	<32	Negative	Negative
H 106	<32	Negative	Negative	<32	Negative	Negative
H 107	<32	Negative	Negative	<32	Negative	Negative
H 108	<32	Negative	Negative	<32	Negative	Negative
H 109	<32	Negative	Negative	<32	Negative	Negative
H 110	<32	Negative	Negative	<32	Negative	Negative
H 111	<32	Negative	Negative	<32	Negative	Negative
H 112	128	**POSITIVE**	Negative	32	**SUSPECT**	Negative
H 113	<32	Negative	Negative	<32	Negative	Negative
H 114	<32	Negative	Negative	<32	Negative	Negative
H 115	<32	Negative	Negative	<32	Negative	Negative
H 116	<32	Negative	Negative	<32	Negative	Negative
H 117	<32	Negative	Negative	<32	Negative	Negative
H 118	<32	Negative	Negative	<32	Negative	Negative
H 119	<32	Negative	Negative	32	**SUSPECT**	Negative
H 121	<32	Negative	Negative	<32	Negative	Negative
H 130	<32	Negative	Negative	<32	Negative	Negative
H 407	<32	Negative	Negative	<32	Negative	Negative
CDFG Control/Host						
H 201	<32	Negative	Negative	<32	Negative	--- [4]
H 202	<32	Negative	Negative	Tortoise is temporarily lost		--- [4]
H 203	<32	Negative	Negative	<32	Negative	Negative
H 204	<32	Negative	Negative	--- [5]	--- [5]	Negative
H 205	<32	Negative	Negative	--- [5]	--- [5]	Negative
Hyundai Site (Outside)						
H 15	128	**POSITIVE**	Negative	64	**POSITIVE**	Negative

1 PCR cultures not yet completed by University of Florida for Year 2006. Year 2005 shown if available. (Some 2005 results have not been supplied by the University of Florida yet.).

2 Unable to extract tortoise on any sampling occasion in 2006. Results shown are from July or October 2005.

3 Tortoise died in 2005. Results shown are from 2005

4. Tortoise lost in 2005 due to early transmitter failure. (Note: AVM Instruments transmitters were used on a portion of the study group initially, but due to untimely transmitter failure and poor operation, they were all replaced with Holohil transmitters.. Some tortoises wearing AVMs were temporarily lost, but re-found through extensive and repeated searches.)

5. ELISA results currently unavailable

Hence, although a negative result does not signal absence, a positive result is definitive for presence of *M. agassizii*.

Condition Indices. Condtion indices for translocated tortoises were similar to both control and host tortoises (Table 3), for both genders, and there is no apparent loss of body mass at one or two years post-translocation that is due to translocation. Females in 2006 emerged from hibernation in slightly better condition than males (although not significant: $P_{1,49} = 0.28$), but following the spring oviposition period, had significantly lower condition indices ($P_{1,49} < 0.001$). These lower condition indices remained into hibernation ($P_{1,49} = 0.009$).

Table 3
Hyundai Desert Tortoise Translocation Project
Comparative Condition Indices ($g/m^3 * 10^{-3}$) for Translocated, Control, and Host Tortoises in Year 2006

Cohort	April		July		October	
	Female	Male	Female	Male	Female	Male
Translocated Tortoises **(both sites)**	1.146	1.145	0.942	1.049	0.818	0.980
BLM Control	1.157	1.114	0.946	1.051	0.880	0.931
Host Tortoises **(CDFG, Translocation SE)**	1.158	1.122	0.931	1.064	0.947	0.987

Tortoise Movement Following Fence Removal

The tortoise fence was detached from the perimeter fence on the first translocation site (Translocation S12) and removed during July 2006. This was 27 months after tortoises had been translocated to that site. It was also prior to the autumn period of high tortoise activity. During the period between fence removal and hibernation, only three tortoises moved off the site. Two of these, Female H24 and Male H04 moved less than 100 meters off the translocation site and then moved back onto the site. H24 finally hibernated less than 50 meters off the site. Female H21 remained on the site until October, when she moved approximately 40 meters off site. She ultimately hibernated approximately 220 meters north of the site. The remaining 12 translocated tortoises remained on the translocation site.

Autumn 2006 followed late June precipitation (1.8 mm) and was accompanied by early October precipitation (2.4 mm), with the resultant germination of several forage species. In addition to normal elevated testosterone levels in the fall, these environmental conditions promoted activity and thereby heightened the opportunity for tortoises to leave the site of translocation. The result that only two tortoises moved a very short distance off the site suggests that, at least in the short term, repatriation of the site is a success. The remaining two years of the study will identify further movement patterns and provide more information on the value of this repatriation technique for re-populating depauperate areas.

CONTINUED STUDIES

The tortoise fence from the second translocation site (Translocation SE) was removed during Winter 2006/7, 22 months following translocation. Tortoises will emerge from hibernation without the constraints of a border fence. Intensive monitoring has begun to help insure that tortoises will not be lost should they move substantial distances. Based on the lack of movement away from the translocation site for the first set of tortoises released (Translocation S12), the second release occurred both earlier and preceding spring, which is generally a period of maximum foraging, as well as nesting, for tortoises. Releasing the translocatees during different seasons and following different time periods since translocation will provide an opportunity to examine repatriation success under different conditions.

The remaining aspects of the Translocation Study are ongoing.

ATTACHMENTS

1. **Initial summary of tortoise translocation from the Hyundai facility**

2. **Initial summary of 2005 tortoise translocation from the Hyundai Proving Grounds**

MEMORANDUM

To: Steve Juarez, Judy Hohman, Nicholas Browning
From: Alice Karl
Date: April 18, 2004

Re: Initial summary of tortoise translocation from the Hyundai facility

This memorandum provides a brief summary of the initial tortoise translocation from the Hyundai facility. A more detailed account, with pictures, will follow when I have access to software for downloading the films and some of the behavioral data have been analyzed.

On April 10 and 11, fifteen tortoises from the Hyundai test track facility were translocated to the one square mile translocation site (Section 12 in Township 31S and Range 39E). This removed all of the tortoises that were currently inside the site boundary (with the exception of one injured animal and one recently found clinically ill animal), plus several that were typically traveling on and off the site and had been observed pacing the fences near the site border. (Note: Because the border of the site is not yet fenced and a substantial amount of disturbance has occurred at the site, many of the currently transmittered 26 tortoises had moved off the site shortly after exiting from hibernation this spring.)

All tortoises were weighed and assessed for clinical signs at the time of translocation. None had clinical signs. Three of the translocated tortoises, captured after serology tests were run last October, have not yet been tested for *Mycoplasma agassizii* exposure. (This was foreseen and is consistent with the translocation plan and HCP.) Serology testing on all animals in the study, including control, translocated, resident, and remaining Hyundai site tortoises, will occur again in approximately one week. (It takes approximately 6-8 weeks after exposure to the pathogen for a tortoise to mount a sufficient titer level for serology tests, so any positive test for exposure to *M. agassizii* will not be the result of translocation.)

Artificial burrows were constructed for all of the tortoises prior to translocation. All tortoises were captured in the late afternoon and released at their burrows at night, when the animals were inactive and largely asleep. Eight of the tortoises were penned with temporary tortoise-proof fencing in approximately 15-foot diameter pens; the remaining seven tortoises were released without pens. Fences were removed for the penned animals at Day 3.

Tortoises were moved in relatively the same geographic configuration as they originally occurred at the Hyundai site, such that a tortoise moving east, for instance, would meet the same tortoise it would have met on the Hyundai site. Two male-female pairs of tortoises were moved together because they were either captured together in the same burrow at the time of translocation or had spent the winter in the same burrow.

Behavioral assessments will follow at a later date, but briefly, tortoises ate, copulated, and have individually either remained at their artificial burrows, occupied other tortoise's artificial burrows, or begun to construct their own burrows; they have moved various distances and directions. Tortoises, while a generalist species, are individual specialists, and their behaviors on this project are no exception to this pattern.

MEMORANDUM

To: Steve Juarez, Judy Hohman, Nicholas Browning
From: Alice Karl
Date: May 8, 2005

Re: Initial summary of 2005 tortoise translocation from the Hyundai Proving Grounds

This memorandum provides a summary of the translocation of the remaining seronegative tortoises originally found on the Hyundai facility. The new translocation site is 1.25 mi^2 and encompasses Section 17 and the southeastern quarter of Section 18 in Township 31S and Range 40E. It abuts the Department Ecological Preserve on the latter's southeastern boundary. The site has been entirely fenced with hog wire (a.k.a. "field fence") to deter intrusion by off-highway-vehicle recreationists. Attached to the lower portion of the fence is ¼ -inch mesh hardware cloth, buried and extending two feet above the ground surface, as a tortoise-proof barrier.

On April 11 and 12, following completion of the tortoise-proof fence around the new translocation site and a search of the entire site for resident tortoises, the twelve remaining seronegative tortoises from the Hyundai test track facility were translocated to the new translocation site. Tortoises were collected in the late afternoon and released at night because this coincides with the time of the day when they are inactive. All were relaxed and remained in their burrows at the time of release.

An approximately 1.5-meter long artificial burrow was constructed for each tortoise prior to translocation. No tortoises were penned at their translocation burrow, as they were in the first translocation effort in 2004. This was based on the observations in 2004 that penned, translocated tortoises spent a substantial amount of time pacing the fence and there was no evidence that penned tortoises had greater burrow fidelity than un-penned tortoises.

Tortoises were moved in relatively the same geographic configuration as they originally occurred at the Hyundai site, such that a tortoise moving east, for instance, could encounter the same tortoise it would have met on the Hyundai site.

All tortoises were watched for at least one full day immediately following release to observe behaviors and insure that no tortoise exhibited behavior that could compromise survival. In fact, the tortoises appeared "relaxed" to all observers and all tortoises spent substantial amounts of time foraging (especially on the abundant *Lotus humistratus*) as well as frequently seeking shade and/or constructing pallets for resting. Two tortoises encountering the boundary fence walked the fence prior to seeking shade. All translocated tortoises continued to be located approximately weekly during April, following this initial observation period. Subsequent locations will be consistent with the translocation plan (i.e., increased locations during high-activity periods; decreased locations during periods when tortoises could be expected to travel shorter distances).

All tortoises were weighed and assessed for clinical signs at the time of translocation. Each had been weighed previously for comparative condition indices to control (un-translocated) tortoises. Serology testing had already been completed in October 2004 on all but one of the translocated tortoises. The remaining tortoise was tested within two weeks of release, however.[5] The eight resident tortoises at the translocation site were also tested at this time. All were seronegative and none had clinical signs.

It should be noted that most tortoises had been foraging on the abundant forage this year since early March. Ample forage still remained at the translocation site at the time of translocation, although it was beginning to senesce. Ambient temperatures remained cool for most of April, so it was generally unnecessary for translocated tortoises to seek burrows for thermal relief.

In accordance with the translocation plan, vegetation data have been collected for comparison between the original capture site (Hyundai Proving Grounds), the translocation sites, and the control site. Comparisons include site characterization (density, frequency, species composition, and percent cover) as well as forage biomass. This, in combination with condition indices (i.e., mass to volume ratios), and activity levels (from data loggers) are currently being analyzed.

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[5] It takes approximately 6-8 weeks after exposure to the pathogen for a tortoise to mount a sufficient titer level for serology tests, so any positive test for exposure to *M. agassizii* will not be the result of translocation.

Reseeding Four Sensitive Plant Species in California and Nevada

H.D. Hiatt
T.E. Olson
J.C. Fisher, Jr.

Abstract–The Kern River Gas Transmission pipeline was constructed in 1991 to supply natural gas to be used in the thermally enhanced recovery of crude oil in Kern County, California, as well as to distribute natural gas in Utah, Nevada, and southern California. Populations of nine sensitive plant species were observed during surveys conducted prior to construction of the pipeline. Mitigation measures for this project included avoidance of identified populations, and reseeding of Rusby's desert mallow (*Sphaeralcea rusbyi* ssp. *eremicola*), Parish's phacelia (*Phacelia parishii*), rosy twotone beardtongue (*Penstemon bicolor* ssp. *roseus*) and yellow twotone beardtongue (*Penstemon bicolor* ssp. *bicolor*). Revegetation success varied within species. The number of Parish's phacelia plants in 1992 that germinated in adjacent seeded and unseeded plots was 706 and 10, respectively. In 1993, the number of plants increased to 2,702 in the seeded plot and 245 plants in the non-seeded plot. During an inventory in 1992, 216 Rusby's desert mallow plants were observed in 73 of 128 standard seeded plots (57 percent), and 300 rosy twotone beardtongue plants were found in the 11 seeded plots.

The Kern River Gas Transmission pipeline (KRGT) was constructed in 1991 to deliver new supplies of natural gas to be used in the thermally enhanced recovery of heavy crude oil in Kern County, California, and also to distribute natural gas in Utah, Nevada, and southern California. The pipeline route extended from a point near Opal, Wyoming, through Utah and Nevada to Daggett, California. Total pipeline length was 596 miles, which included 119 miles in Nevada and 95 miles in California.

The Final Environmental Impact Report/Environmental Impact Statement (Chambers Group 1987) identified potential habitat for several rare plant species along the proposed pipeline route. Additional information regarding rare plants in Nevada and California was acquired during 1989 and 1990 field surveys (Dames & Moore 1990a, b). Those surveys followed a mitigation plan developed by Dames & Moore (1990c). Potential species of special concern included federal candidate species, state-listed species and species on the Northern Nevada Native Plant Society (NNNPS) and California Native Plant Society (CNPS) lists of rare plants (United States Fish and Wildlife Service 1990; NNNPS 1989; Smith and Berg 1988). One sensitive plant species was found in April 1991, after construction began, and further mitigation measures were developed.

The objective of this paper is to document implementation of mitigation measures regarding reseeding of four taxa of sensitive plants along the Nevada and California portions of the Kern River pipeline route and the subsequent reestablishment of these sensitive populations.

Sensitive Plant Surveys and Mitigation Measures

During sensitive plant surveys conducted in 1989 and 1990 along the Kern River pipeline route in Nevada and California, populations of nine sensitive species were observed within the 200-foot wide survey corridor (Table 1). The pipeline was generally constructed in a 75-foot wide disturbance zone located within the survey corridor. These populations were described and mapped (Dames & Moore 1990a, b). Additional surveys were conducted in May 1991 to locate *Phacelia parishii*.

Mitigation measures for this project to facilitate reestablishment of sensitive plants included avoidance, minimization of disturbance to the extent practicable, salvage of topsoil, use of an imprinter during reclamation, and reseeding. Seedbank material, including seeds of sensitive plants saved along with the topsoil, assisted in reestablishment of rare plants. Similarly, the use of an imprinter aided in the retention of precipitation, which assisted the revegetation of both common and sensitive plants.

Active revegetation measures were evaluated for their appropriateness in reestablishing sensitive plants. The methods evaluated for potential use included reseeding of sensitive species, and transplanting bearclaw poppy (*Arctomecon californica*). Mormon needle grass (*Stipa arida*) and scaly cloak fern (*Cheilanthes cochisensis*) plants were located at or adjacent to the 200-foot wide corridor, and avoidance of plants was considered more appropriate than reseeding. The same consideration applied for the annual species three corner milk vetch (*Astragalus geyeri* var. *triquetrus*) and sticky buckwheat (*Eriogonum viscidulum*) which were observed outside of the standard 75-foot-wide disturbance zone and work spaces. In anticipation of possible transplantation efforts, a permit to collect 50 bearclaw poppy plants was obtained from the Nevada Division of Forestry. However, because reseeding and transplanting

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In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Hermi D. Hiatt, Biologist, Dames & Moore, Las Vegas, Nevada; Thomas E. Olson, Biologist, Dames & Moore, Santa Barbara, California; Jack C. Fisher, Jr., deceased.

Table 1—Sensitive plant species observed along the Kern River pipeline route, Nevada and California, 1989 to 1991.

Taxon name	Common name	Protection status
Sphaeralcea rusbyi ssp. *eremicola*	Rusby's desert mallow	C2, CNPS 1B
Phacelia parishii	Parish's phacelia	C2, CNPS 1B*
Penstemon bicolor ssp. *roseus*	Rosy twotone beardtongue	C2
Penstemon bicolor ssp. *bicolor*	Yellow twotone beardtongue	C2
Stipa arida	Mormon needle grass	CNPS 2
Cheilanthes cochisensis	Scaly cloak fern	CNPS 2
Astragalus geyeri var. *triquetrus*	Three corner milkvetch	C2, Nevada CE, NNNPS T
Eriogonum viscidulum	Sticky buckwheat	C2, Nevada CE, NNNPS T
Arctomecon californica	Bearclaw poppy	C2, Nevada CE, NNNPS T

*Currently reclassified to CNPS 2; CNPS = California Native Plant Society; NNNPS = Northern Nevada Native Plant Society.

of this species has not been successful in the past (Knight 1990), those methods were not implemented. The remaining four sensitive plant taxa were located within the pipeline zone and could not be avoided during construction of the pipeline. These species were Rusby's desert mallow (*Sphaeralcea rusbyi* sp. *eremicola*), Parish's phacelia (*Phacelia parishii*), rosy twotone beardtongue (*Penstemon bicolor* ssp. *roseus*) and yellow twotone beardtongue (*Penstemon bicolor* ssp. *bicolor*). Reseeding of these species appeared to be appropriate and the methods are described below.

Reseeding Methodology

Seed Collection and Storage

Reseeding efforts were accomplished for Rusby's desert mallow, Parish's phacelia, rosy twotone beardtongue, and yellow twotone beardtongue. Ripe seeds of Rusby's desert mallow were collected on 20-21 June, 1991. This species is located near Keany Pass on the east and west sides of the Clark Mountains, San Bernardino County, California, approximately 10 miles west of the Nevada/California border and Interstate 15. Seed collections for this species were segregated as east and west side samples to maintain local gene pools. Seed material for Parish's phacelia was collected on 21 May, 1991. Seeds were gathered from a larger population located less than one mile north of the population that intercepted the pipeline near the Manix Trail, approximately 12 miles northeast of Yermo, California. Collections of seeds of the two subspecies of twotone beardtongue were accomplished during July 1990, within and adjacent to locations along the proposed pipeline construction zone in which the subspecies were observed during the initial plant surveys. Rosy twotone beardtongue seeds were collected near Apex, Clark County, Nevada, at the intersection of the pipeline and State Highway 93. Yellow twotone beardtongue seeds were collected in a wash about 0.5 mile northeast of Wilson Tank in the Bird Spring Range, approximately 8 miles north of Goodsprings, Nevada.

Seeds of all taxa were air dried and stored at constant temperature (approximately 65 to 70 °F). Seed material of Rusby's desert mallow and Parish's phacelia was not cleaned and contained capsules, small leaves and some stems, but seeds of the two subspecies of twotone beardtongue were cleaned by removing most of the extraneous plant matter.

Seed viability of the four taxa was tested by either the Ransom Seed Laboratory in Carpinteria, California, or the Colorado Seed Laboratory at Colorado State University in Fort Collins, Colorado. The following tests were performed to obtain the percentage of total live seed. Germination tests resulted in 1 to 2 percent germination within 21 days for Rusby's desert mallow seeds, and 0 to 6 percent within 14 days for Parish's phacelia seeds. The remaining seeds were treated with gibberellic acid and 5 to 50 percent of the seeds germinated (percent hard seed, as shown in Table 2). Ungerminated Parish's phacelia seeds were then evaluated for viability with tetrazolium. The two subspecies of twotone beardtongue were only tested with tetrazolium, resulting in 83 to 87 percent total live seed (Table 2).

Reseeding Rusby's Desert Mallow

Rusby's desert mallow, a perennial herb, was reseeded in late October and early November, 1991. Seventy-two reseeding plots (designated as E-1 through E-72) were placed in the disturbance zone on the east side of Keany Pass. Plots E-1 to E-8 were 6-foot diameter circles, and the remaining sites were 8 feet in diameter. Seven or eight plots each were placed within 10 of 11 drainages in that portion of the right-of-way. For the purpose of placing the sample plots, a drainage was defined as the area from hilltop to hilltop. West of Keany Pass, 52 plots were placed within approximately a one-mile stretch of pipeline (plots W-1 to W-52), and 5 plots were placed in the area of a disjunct population (plots W-53 to W-57) approximately 2.25 miles west of Keany Pass. Sample plots W-1 to W-20 were 8 feet in diameter, and the remaining plots each covered a 4-foot diameter circle. The 5 plots in the area of the disjunct population were placed on a west-facing slope; the other 52 sample plots were placed within 11 drainages on both east- and west-facing slopes. Each plot was marked with rebar and metal tags.

Because of pipe repair, the seed material in sample plots E-5 and E-8 was salvaged subsequent to reseeding. Topsoil and seed material were removed from those two sample sites in November 1991, and new plots were established 2 weeks

Table 2—Results of germination tests for seeds collected along the Kern River pipeline route in Nevada and California, 1991.

Species	Sample number	% Germination	% Hard seed	% Tetrazolium	% Total live seed
Rusby's desert mallow (east side)	#1	1	44	—	45
	#2	2	50	—	53
Rusby's desert mallow (west side)	#1	1	9	—	10
	#2	1	5	—	6
Parish's phacelia	#1	3	39	17	59
	#2	6	17	51	74
	#3	0	22	55	77
Rosy twotone beardtongue	#1	—	—	85	85
Yellow twotone beardtongue	#1	—	—	83	83
	#2			87	87

later. The soil was deposited within a new 4-foot diameter circular area in the vicinity of the old plot sites.

Each plot was raked prior to reseeding to loosen compacted soils. Seed material (0.5 ounce) was broadcast by hand in each sample plot and the ground was raked again to cover seeds with a small amount of soil. Seed material was estimated to contain approximately 1,190 Rusby's desert mallow seeds per 0.5 ounce. Thirty-six ounces of material were broadcast on the east side of Keany Pass, and 29 ounces on the west side. Overall, it was estimated that approximately 155,000 seeds were dispersed in the Clark Mountain area.

Reseeding Parish's Phacelia

Before reseeding the annual Parish's phacelia, special preparation of the reseeding plot was implemented. This species generally grows on desert alkaline flats, specifically in desiccation cracks of thick clay accumulations. A reseeding plot of 270 by 30 feet was chosen on the spoilside of the pipeline within the 75-foot wide disturbance zone. The plot was sprayed with 4,000 gallons of water on 3 December, 1991. Then the site was allowed to dry and crack. An equally large unwatered control plot was chosen on the workside of the pipeline within the disturbance zone. After 2 weeks, the soil had dried and cracked and the habitat of the reseeding plot approached nearly natural conditions. Transects were walked width-wise, and the seed material was evenly broadcast in 25 subsamples. Seeds were distributed for an additional 10 feet beyond the disturbed area, to compensate for depletion of plants during seed collection. It was estimated that approximately 1,300,000 Parish's phacelia seeds were broadcast during reseeding. The plot was marked with rebar and metal tags. To reduce motor vehicle travel through the plot, orange wooden stakes were placed across the width of the plot.

Reseeding Twotone Beardtongue

Reseeding of the two perennial subspecies of twotone beardtongue was accomplished in early November 1991. Reseeding areas were selected according to the general location of collection to maintain local gene pools. In addition, existing populations were located near the pipeline before reseeding within the disturbance zone.

Rosy twotone beardtongue was reseeded near the intersection of the pipeline and Highway 93. Five sites were chosen within the 0.5-mile stretch west of the highway. Seeds were dispersed within 11 three-foot diameter subplots. At Site 1, which is located at the greatest distance from the highway, 1 subplot was established at the southern edge of the pipeline disturbance. Site 2 was established in a prominent wash approximately 0.4 miles from the highway. Three subplots were placed across the disturbance zone, with additional plots east of the wash. One subplot each was placed at the northern edge of the pipeline disturbance at Sites 3 and 4, located approximately 2,000 and 1,800 feet from the highway, respectively. Site 5 consisted of 2 subplots at the northern edge of the disturbance zone and a broad wash adjacent to Highway 93. Approximately 30,600 rosy twotone beardtongue seeds were broadcast in the 11 subplots.

Yellow twotone beardtongue was reseeded in a small wash dissecting the disturbance zone approximately 0.5 miles northeast of Wilson Tank in the Bird Spring Range. An approximately 115-by-53-foot plot was established and marked at the corners. The equivalent of 45 subplots of 9 to 16 square feet was established within the large plot. Individual subplots were raked and a small amount of seed was spread within the subplot. The subplots were then raked to cover the seed. Approximately 17,400 seeds were broadcast.

Reseeding Results

Reseeding success was evaluated by inventorying plant establishment the first season after reseeding activities. One species was evaluated for a second season. The survey methods and the results of reestablishment of each species are described below.

Rusby's Desert Mallow

The 57 plots located on the west side of the Clark Mountains were inventoried on 21 June and 9 August, 1992.

Table 3—Results of follow-up surveys of Rusby's desert mallow, Clark Mountains, San Bernardino County, California, June, August 1992.

	Side of Keany Pass			
	Standard plot		Expanded plot	
	East	*West*	*East*	*West*
Plots surveyed	71	57	71	57
Total plants observed	69	147	84	237
Plants/Plot	1.0	2.6	1.2	4.5
Frequency (%)	46	70	46	72
Density (plants/100 ft^2)	2.0	3.8	—	—

Seventy-one of 72 plots on the east side of the Clark Mountains were inventoried on 20 June, 1992. Locations of these plots were identified by markers that had been installed during reseeding. The boundaries of the plots were determined by observing the rake marks that were still discernible, and by measuring from the center stake. Plot E-5 was not found during the inventory.

Many Rusby's desert mallow plants were observed, sometimes in greater densities in areas adjacent to the reseeded plots. It was speculated that seeds were transported outside of the reseeded plots by wind and rain erosion of the seedbed. As a result, counts were made in the original reseeded plot as well as in an expanded plot of approximately 40 feet in diameter.

The total number of plants counted in the original plots was 69 plants on the east side of the Clark Mountains and 147 plants on the west side (Table 3). The east-side plots contained an average of 1.0 plants, and 33 of the 71 plots contained at least 1 plant. The average number of plants per plot of the west side was 2.6 plants. Growth of at least 1 plant occurred in 40 of 57 plots. The average densities of plants in the east side and west side plots were 2.0 per 100 square feet and 3.8 per 100 square feet, respectively.

In the expanded plots, 84 plants were counted on the east side of the Clark Mountains and 237 plants on the west side. The average number of plants per plot was 1.2 (east) and 4.5 (west), respectively. The number of plots that contained at least 1 plant was almost the same as in the original plots, as shown in Table 3. Frequency of the original and expanded plots was 46 percent in the east side plots, and 70 and 72 percent on the west side.

Parish's Phacelia

Reestablishment of Parish's phacelia was evaluated on 18 April, 1992, and during April 1993. In addition to the reseeded plot, two additional plots were inventoried as control sites. One control site was located within the disturbance zone of the pipeline; it had not been reseeded in 1991. The other control plot was located in an undisturbed area outside the disturbance zone. Each plot measured 270 by 30 feet. The number of Parish's phacelia plants observed in each plot was counted. The first year after reseeding, 706 Parish's phacelia had germinated in the reseeded plot, and only 2 plants in the control plot within the disturbance zone (Table 4). In the adjacent non-reseeded plot, a total of 10 plants was found. In 1993, approximately 2,702 plants were found in the reseeded plot, which represented a density of 33.4 per 100 square feet. In the non-reseeding plots in and adjacent to the disturbance zone, 245 plants and 1,014 plants were counted, respectively.

Rosy Twotone Beardtongue

The 5 reseeding sites were inventoried on 6 October, 1992. Locations of the plots were identified by markers that had been installed during reseeding activities. Although many of the sites had been disturbed by off-road vehicle traffic, 10 of the 11 subplots contained small plants, ranging from 3 to 68 per subplot (Table 5), with a total of 300 plants. In the following year, no counts were made. However, cursory observation indicated that plants were flowering and covered the entire surface of one three-foot diameter subplot. Other subplots were less prolific.

Yellow Twotone Beardtongue

During the October 1992 inventory, the reseeding plot and surrounding area contained a moderate to dense cover of species of a wild horse seed mix, including *Penstemon* sp. seedlings. Subsequent to the sensitive species reseeding effort in 1991, the pipeline disturbance zone in that area was reseeded with a different seed mixture. The second reseeding effort was completed at the request of the Bureau of Land Management with the objective of enhancing the wild horse habitat in that area. The yellow twotone beardtongue reseeding area was included in the second reseeding effort. The wild horse seed mix contained Palmer's

Table 4—Results of follow-up surveys of Parish's phacelia, San Bernardino County, California, April 1992 and April 1993.

	Within disturbance zone		Adjacent to disturbance zone
	Reseeded	Non-reseeded	Non-reseeded
1992			
Number of plants	706	2	10
Density (plants/100 ft^2)	8.7	<0.1	0.1
1993			
Number of Plants	2,702	245	1,014
Density (plants/100 ft^2)	33.4	3.0	12.5

Table 5—Results of follow-up surveys of rosy twotone beardtongue, Clark County, Nevada, October 1992.

Site	Number of subplots	Number of plants observed/subplot
1	1	45
2	6	0-45
3	1	55
4	1	68
5	2	3-26
Total	11	300

penstemon (*Penstemon palmeri*). Yellow twotone beardtongue could not be distinguished from Palmer's penstemon at this morphological stage, and reseeding efforts were not determined.

Discussion and Conclusions

Review of this project indicated successful mitigation for impacts to sensitive plant species. Avoidance and minimization of disturbance zones is still considered the preferred method, but active revegetation in the form of reseeding can be an effective mitigation alternative for some species if avoidance is not possible.

Early planning is important for successful reestablishment of sensitive plant species. Several points need to be considered. These are: site analysis of habitat prior to disturbance; biotic and physical requirements of each taxon; optimal time for seed collection; specific site preparation to create an environment favorable for reestablishment; and developing methods of monitoring.

Reseeding of Rusby's desert mallow required no specific seedbed preparation. This species appears to be adapted to disturbed areas; many of the seeds collected came from plants found on old powerline spur roads. Other factors, however, may have influenced the difference in reestablishment between the east and west populations (2.0 plants versus 3.8 plants per 100 square feet, respectively). Specifically, the one-time seed collection was apparently suboptimal. Seeds appeared to be at a late stage of seed dispersal; the west side population was further advanced than the east side population. In addition, the east side material contained 50 percent hard seeds compared to 10 percent in the west side population. Since afterripening may break dormancy over time (Young and Young 1986), a second year of monitoring may have been beneficial. Also, seed collections should have occurred over a period of time to obtain high quality seeds.

Some species require special methods for seedbed preparation. For instance, the disturbance zone was graded and leveled at the end of construction. Parish's phacelia specifically grows in desiccation cracks of thick clay accumulations, and re-creating this microenvironment was critical for reestablishment. Because rain is unpredictable in desert environments, application of 4,000 gallons of water was essential for re-creating desiccation cracks. During the second year after reseeding, natural seed dispersal and subsequent rains to create desiccation cracks in the control plots apparently increased seed germination in both the reseeding and control plots.

Frequently, provisions are not made for monitoring the success of reestablishment projects, for both sensitive and common species. Hall (1987) reported that 7 of 15 mitigation projects failed because of lack of maintenance and monitoring. No monitoring was required for this project, neither of the sensitive plant taxa nor of the imprinting success and natural revegetation of the common species. Monitoring the reseeding results of these four taxa was only due to a voluntary effort of the authors. Valuable information could be gained from revegetation projects, if monitoring the success rate would be a condition of project approvals by the responsible governmental agencies.

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Conservation Ecology **6**(1): 11. [online] URL: http://www.consecol.org/vol6/iss1/art11

CONSERVATION
ECOLOGY

Synthesis

Human-caused Disturbance Stimuli as a Form of Predation Risk

Alejandro Frid[1] and Lawrence Dill

ABSTRACT. A growing number of studies quantify the impact of nonlethal human disturbance on the behavior and reproductive success of animals. Athough many are well designed and analytically sophisticated, most lack a theoretical framework for making predictions and for understanding why particular responses occur. Behavioral ecologists have recently begun to fill this theoretical vacuum by applying economic models of antipredator behavior to disturbance studies. In this emerging paradigm, predation and nonlethal disturbance stimuli create similar trade-offs between avoiding perceived risk and other fitness-enhancing activities, such as feeding, parental care, or mating. A vast literature supports the hypothesis that antipredator behavior has a cost to other activities, and that this trade-off is optimized when investment in antipredator behavior tracks short-term changes in predation risk. Prey have evolved antipredator responses to generalized threatening stimuli, such as loud noises and rapidly approaching objects. Thus, when encountering disturbance stimuli ranging from the dramatic, low-flying helicopter to the quiet wildlife photographer, animal responses are likely to follow the same economic principles used by prey encountering predators. Some authors have argued that, similar to predation risk, disturbance stimuli can indirectly affect fitness and population dynamics via the energetic and lost opportunity costs of risk avoidance. We elaborate on this argument by discussing why, from an evolutionary perspective, disturbance stimuli should be analogous to predation risk. We then consider disturbance effects on the behavior of individuals—vigilance, fleeing, habitat selection, mating displays, and parental investment—as well as indirect effects on populations and communities. A wider application of predation risk theory to disturbance studies should increase the generality of predictions and make mitigation more effective without over-regulating human activities.

INTRODUCTION

More than 30 years ago, Walther (1969) published an experiment in which he assumed that animals perceive human disturbance similarly to predation risk. Walther approached Thomson's gazelles (*Gazella thomsoni*) with his car to test whether flight initiation distance (the distance between the predator and prey at which prey begin to flee) depended on age, sex, and social status. He also studied gazelles fleeing from wild dogs (*Lycaon pictus*) and other predators, and appeared satisfied that the variables affecting responses to a car would have been similar had the stimuli been actual predators (Walther 1969). Walther's experiment was stimulated by the work of Hediger (1934, cited in Walther 1969), who three decades earlier had approached African ungulates with a car to determine interspecific differences in flight initiation distance.

Since these pioneering studies, research on disturbance has begun to embrace the principle that nonlethal disturbance stimuli caused by humans are analogous to predation risk. The notion works because responses both to predation risk (Lima and Dill 1990, Lima 1998) and to disturbance stimuli (e.g., Gutzwiller et al. 1994, Steidl and Anthony 2000) divert time and energy from other fitness-enhancing activities such as feeding, parental care, or mating displays. (In the context of our argument, *disturbance* denotes a deviation in an animal's behavior from patterns occurring without human influences. We use the term *disturbance stimulus* for a human-related presence or object [e.g., birdwatcher, motorized vehicle] or sound [e.g., seismic blast] that creates a *disturbance.*) Animals optimize these trade-offs when their investment in antipredator behavior tracks short-term changes in predation risk (Lima and Dill 1990, Lima 1998). For example, woodchucks (*Marmota monax*) decrease their flight initiation distance when thry are closer to a refuge burrow (Bonenfant and Kramer 1996); and gray squirrels (*Sciuris carolinensis*) show the same response when nearer to a refuge tree (Dill and Houtman 1989). Individuals near a refuge that tolerate closer approaches by potential predators avoid

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fleeing costs (abandoning a feeding site and expending energy on locomotion) that do little to increase safety (see Ydenberg and Dill 1986). The plasticity of flight initiation distance is based on the same economic principle—optimization of trade-offs—that drives antipredator behavior in general (Lima and Dill 1990, Lima 1998).

When encountering disturbance stimuli, ranging from the dramatic, low-flying helicopter to the quiet wildlife photographer, an animal's response should follow the same economic principles used by prey encountering predators (Berger et al. 1983, Madsen 1994, Gill et al. 1996, 2001, Gill and Sutherland 2000). We call this verbal model the risk-disturbance hypothesis. It predicts that responses by disturbed animals track short-term changes in factors characterizing disturbance stimuli, with responses being stronger when perceived risk is greater. The level of perceived risk may result from a combination of factors that characterize disturbance stimuli, along with factors related to natural predation risk (e.g., Frid 2001*a,* Papouchis et al. 2001).

Although earlier work (notably, Berger et al. 1983, Madsen 1994) used predation risk as an analogy for understanding human disturbance of wildlife, Gill and Sutherland (2000) explicitly argued that disturbance stimuli and predation risk indirectly affect survival and reproduction through trade-offs between perceived risk and energy intake. Their models predict how density-dependent processes interact with food distribution and disturbance stimuli to determine habitat shifts and population dynamics (Gill et al. 1996, 2001, Gill and Sutherland 2000).

Here we develop the risk-disturbance hypothesis further. We discuss why, from an evolutionary perspective, disturbance stimuli should be analogous to predation risk. Most disturbance studies focus on responses directly related to energy trade-offs: fleeing, vigilance, and habitat selection. We use examples from that rich literature to assess some predictions of the risk-disturbance hypothesis. We also use a predation risk framework to explore four areas in which disturbance effects are less studied: mate acquisition, parental investment, population dynamics, and interactions at the community level. Finally, we evaluate when and how disturbance studies might increase their conservation value by applying the risk-disturbance hypothesis.

ARE DISTURBANCE STIMULI REALLY ANALOGOUS TO PREDATION RISK?

A devil's advocate might argue that disturbance stimuli are not analogous to predation risk because prey have evolved predator-specific antipredator behaviors (e.g., Walther 1969, Ghalambor and Martin 2000), and many disturbance stimuli (e.g., aircraft) are too recent for animal responses to reflect adaptive programming. However, prey have evolved antipredator responses to generalized threatening stimuli, such as loud noises and rapidly approaching objects (e.g., Dill 1974*a, b*). Prey respond when such stimuli cross a threshold, even when the specific source is new to the prey's evolutionary history (e.g., introduced predators or motorized vehicles). The zebra danio (*Brachydanio rerio*), a small fish, provided one extreme example when exposed to real predators (largemouth bass: *Micropterus salmoides*), a predator-shaped model, and a 'cinematographic' predator (a film of a black dot increasing in size, simulating an approaching object). In all three cases, danios fled when the angle subtended by the predator at the prey's eye reached a threshold rate of change (see Appendix 1). This threshold 'loom' rate depended on the size and speed of the approaching 'predator', and responses were qualitatively similar for the different 'predator' types. In other words, danios appeared to decide the timing of fleeing by relating the loom rate to a margin of safety, regardless of whether the predator was real, a model, or a film (Dill 1974*a, b*).

A devil's advocate might also argue that predation risk and disturbance stimuli are not analogous because disturbed animals do not necessarily risk direct mortality. The counter-argument is that it is irrelevant if disturbance stimuli are nonlethal because predation risk differs from predation itself. Although death is the outcome of predation, the outcome of predation risk is a decision made by prey to compromise the rate of resource acquisition or other activities to reduce the probability of death (Abrams 1993, Hugie and Dill 1994, review in Lima 1998). Specifically, predation risk results from the interaction of factors that affect attack and capture probabilities, mainly (1) the structure of the environment, including the distribution of vegetation cover where predators might hide and of refuges where prey might escape, (2) social factors, including the prey's group size and position in the group, (3) the distribution and abundance of predators, and (4) the behavior of predators (whether they are searching for and selecting a given prey type). Because antipredator behavior responds to changes in these factors rather than to predation rate per se, it is reasonable to expect responses to nonlethal disturbance stimuli to follow the same decision rules as responses to predation risk.

Does habituation invalidate this premise? Shouldn't prey that behave optimally recognize that nonlethal stimuli do not warrant the costs of antipredator behavior? Animals rarely have perfect information, and generally are expected to maximize fitness by overestimating rather than underestimating risk. Overestimation costs, such as lost feeding opportunities, have milder fitness consequences than the cost of underestimating danger, which might be immediate death (Bouskila and Blumstein 1992). Thus, habituation to disturbance stimuli, although it generally occurs to some extent, often is partial (e.g., Burger and Gochfeld 1981, 1990, Steidl and Anthony 2000) or negligible (e.g., Berger et al. 1983, Bleich et al. 1994). It is unlikely to disprove the risk-disturbance hypothesis in most situations, even for animals that provide archetypal examples of habituation, such as urban corvids (Ward and Low 1997). Furthermore, there are instances in which antipredator-type responses to nonlethal stimuli should become stronger with repeated exposure to such stimuli. For example, prey learn to associate the low loom rate of an approaching predator that is still far away with the faster loom rate that occurs once the predator is closer. Thus, flight initiation distance or vigilance might increase with repeated exposure to a nonlethal stimulus if the latter is sufficiently aversive (Dill 1974b).

A final issue to consider is that human hunters have represented a real threat to some species over evolutionary time. Thus, in some cases such as people on foot approaching large vertebrates, disturbance stimuli and true predatory stimuli may be indistinguishable from the animal's perspective.

TRADE-OFFS DIRECTLY RELATED TO ENERGY GAIN

We next use the rich literature dealing with disturbance effects on fleeing, vigilance, and habitat shifts to assess some predictions of the risk-disturbance hypothesis. Our assessment is not a quantitative test based on a random sample of the literature, which could be biased by failure to publish negative results. Rather, it is based on selected references and is meant to demonstrate the explanatory value of the hypothesis and to stimulate future studies explicitly designed to test its predictions. We have not included all examples known to us, but only enough to illustrate our arguments.

Fleeing

Prey that have detected a potential predator should make optimal fleeing decisions that balance the benefits of reducing capture probability against the costs of abandoning a resource patch and expending energy on locomotion (Ydenberg and Dill 1986). Fleeing probability should increase when the predator approaches more directly, because a direct approach may convey detection and intent to capture (Burger and Gochfeld 1981, 1990, Cooper 1997, 1998). Although the angle of approach is two-dimensional in some systems (e.g., terrestrial animals on flat ground), in others it has horizontal and vertical components. For instance, an aerial predator may change the approach angle by shifting its elevation relative to prey (rather than lateral distance). The same principle applies to aircraft disturbance, or when ground disturbance stimuli approach animals on landscapes with a vertical dimension (e.g., mountain slopes, trees). The angle of approach is a geometric correlate of the nearest distance between the trajectory of the approaching stimulus and the animal being approached. Thus, greater distances (lateral and vertical) correspond to larger angles and less direct approaches. Angles are more difficult to measure than distances, and most field studies quantify the latter.

Fleeing probability or flight initiation distance should increase when predators are larger or approach faster because prey will experience the loom rate that triggers flight at greater distances (Dill 1974*a*). Flight initiation distance increases as distance to a refuge becomes greater because risk of capture increases (Ydenberg and Dill 1986, Dill and Houtman 1989, Bonenfant and Kramer 1996). Prey may also respond to predator group size. For instance, Thomson's gazelles had smaller flight initiation distances when approached by single hyenas (*Crocuta crocuta*) than when approached by packs (Walther 1969). Flight initiation distance and fleeing probability also increase when prey are at a site that is poor in resources (e.g., little food), because the benefits of clinging to a resource patch are less likely to outweigh the risk of remaining (see data on waterstriders, *Gerris remiges*,, in Ydenberg and Dill 1986).

Predictions of the risk-disturbance hypothesis stimulated by studies of fleeing responses to predators include the following. Fleeing probability and flight initiation distance increase when disturbance stimuli (A) approach more directly, (B) approach more quickly, and (C) are larger in size. They also increase when (D) distance from refuge is greater, (E) group size of the disturbers is greater, and (F) the costs of fleeing are lower. Lower fleeing costs might arise when the resource patch is poor (i.e., less is lost by leaving), rich resources are evenly distributed and easy to locate elsewhere, or environmental conditions (temperature, snow depth) are mild at the time of disturbance, thereby not increasing locomotion costs (see Ydenberg and Dill 1986). We did not consider obstructive cover because it represents a constraint to early detection rather than an influence on the decision to withhold fleeing. Also, we did not consider the effects of group size of disturbed animals, which are difficult to predict due to the opposing effects of dilution and additional sensory organs (Ydenberg and Dill 1986).

Reviewed studies were consistent with Prediction A. Fleeing probability increased for Dall's sheep *Ovis dalli dalli* (Frid 2001*a, b*), ringed seals *Phoca hispida* (Born et al. 1999), and Pacific Brant *Branta bernicla nigricans,* and Canada Geese *B. canadensis* (Ward et al. 1999) as a helicopter or fixed-wing aircraft approached more directly. Bald eagles (*Haliaeetus leucocephalus*) perched on trees alongside a river were more likely to flee from a paddle raft when perches were closer to the river or lower in height (Steidl and Anthony 1996). Table 1 summarizes these and additional examples.

Table 1. Literature examples for assessing predictions concerning fleeing responses. Predictions were that fleeing probability or flight initiation distance increase when disturbance stimuli (A) approach more directly, (B) approach more quickly, and (C) are larger in size. They also increase when (D) distance from refuge is greater, (E) group size of disturbers is greater, and (F) fleeing costs are lower (see *Fleeing* for details).

Study	Species	Stimuli	Predictions		
			Supported	Rejected	Not tested or controls lacking
Born et al. (1999)	ringed seal	helicopter and fixed-wing aircraft	A, F		B, C, D, E
Burger (1998)	Common Tern	motorized watercraft	A, B		C, D, E, F
Burger and Gochfeld (1998)	Louisiana and Little Blue Herons	people on foot	A, E		B, C, D, F
	other waterbird spp.		A	E	B, C, D, F
Delaney et al. (1999)	Mexican Spotted Owl	helicopter	A, F		B, C, D, E
Frid (2001*a,b*)	Dall's sheep	helicopter, fixed-wing aircraft	A, D		B, C, E, F
Hamr (1988)	chamois	hikers, skiers	E, F		A, C, B, D
Lafferty (2001)	Snowy Plover	people on foot	A	B, E	C, D, F
Papouchis et al. (2001)	bighorn sheep	hikers, bikers, vehicles	A, D	E	B, C, F
Steidl and Anthony (1996)	Bald Eagle	paddle raft	A*	A*	B, C, D, E, F
Swarthout and Steidl (2001)	Mexican Spotted Owl	single hiker	A		B, C, D, E, F
Ward et al. (1999)	Pacific Brant and Canada Goose	helicopter and fixed-wing aircraft	A		B, C, D, E, F

*The prediction was supported for fleeing probability, but not flight initiation distance.

Flight initiation distance has been found to increase as lateral distance from the disturbance stimulus becomes greater (e.g., Steidl and Anthony 1996, Frid 2001*a.* These results apparently reject prediction A, but geometric correlations could confound interpretation. Flight initiation distance cannot be smaller than the nearest distance between the animal and the trajectory of the stimulus. Thus, if animals flee when the stimulus is nearest to them, flight initiation distance during indirect approaches will always be larger than during direct approaches. Future analyses need to consider potential artifacts that could arise from this geometric correlation.

Support for Prediction B was inconsistent (Table 1). Supporting the prediction, more Common Terns (*Sterna hirundo*) fled their nests when motorized watercraft approached more quickly (Burger 1998). Contradicting the expectation that earlier fleeing is triggered by a higher velocity (Dill 1974*a,* joggers were less disturbing to Western Snowy Plovers (*Charadrius alexandrinus nivosus*) than were people walking, even after distance to the stimulus was controlled (Lafferty 2001). Future work should analyze whether, under certain conditions, slower disturbance stimuli are analogous to a stalking predator and are perceived as more damgerous than a faster stimulus.

We could not evaluate Prediction C. Although comparisons exist between the effects of aircraft of different sizes, noise level is an important covariate (e.g., Ward et al. 1999) that probably confounds size effects.

The two reviewed studies with relevant data supported Prediction D (Table 1). During indirect approaches by helicopters, Dall's sheep far from rocky slopes were much more likely to flee than were sheep on rocky slopes (Frid 2001*a,*), which provide a refuge from cursorial predators (e.g., Berger 1991). Distance from a refuge probably affects how sheep perceive risk from the generalized stimulus of a large object approaching rapidly, rather than from a perceived aerial predator per se. Ground disturbance had similar effects: bighorn sheep (*Ovis canadensis*) disturbed by hikers, bikers, or road traffic had stronger fleeing responses when farther from rocky slopes (Papouchis et al. 2001).

Support for Prediction E was inconsistent (Table 1). Little Blue Heron (*Egretta caerulea*) and Louisiana Heron (*E. tricolor*) were more likely to flee when birdwatchers were in larger groups. Other species of waterbirds, however, did not respond to disturber group size (Burger and Gochfeld 1998). Flight initiation distance and distances fled by chamois (*Rupicapra rupicapra*) approached by hikers increased with hiker group size (Hamr 1988). Disturber group size of hikers, mountain bikers, and vehicles did not influence fleeing responses by bighorn sheep, however (Papouchis et al. 2001).

Several studies were consistent with Prediction F (Table 1). Ringed seals disturbed by aircraft were more likely to abandon a haul-out site on the ice pack and dive into the sea when the thermal benefits of staying hauled out were lower due to higher wind chill (Born et al. 1999). Mexican Spotted Owls (*Strix occidentalis lucida*) did not flee from helicopters when attending young at their nest, but fled readily during the postfledging period (Delaney et al. 1999). Chamois were more reluctant to flee when deep snow entailed a high cost to locomotion (Hamr 1988).

Vigilance and related activity shifts

A vast literature indicates that prey are more vigilant when the perceived risk of predation is greater. This response increases the chances that the prey will avoid capture, but at the cost of reducing time spent foraging or engaged in other activities. Antipredator vigilance responds not only to the mere presence or absence of predators, but also to factors affecting the level of perceived risk, including group size, distance from a refuge, and obstructive cover (see reviews in Elgar 1989, Lima 1998).

Studies of antipredator vigilance, as well as our discussion on angle of approach from the previous section, stimulated the following predictions. More time is spent vigilant, or less time is spent foraging or resting, when disturbance stimuli (A) approach more directly, (B) remain at closer distances, (C) have a greater group size (e.g., more ecotourists), and (D) occur concurrently with a greater level of natural predation risk (e.g., animals are in smaller groups, closer to obstructive cover, farther from refuge).

The reviewed studies were consistent with Prediction A (Table 2). For instance, vigilance responses or disruptions of resting and foraging by bighorn sheep (Stockwell et al. 1991), Dall's sheep (Frid 2001*b,*) began earlier and lasted longer when aircraft approached more directly.

Table 2. Literature examples for assessing predictions concerning vigilance responses. Predictions were: more time is spent vigilant or less time is spent foraging or resting when disturbance stimuli (A) approach more directly, (B) remain at closer distances, (C) have a greater group size (e.g., more ecotourists), and (D) occur concurrently with a greater level of natural predation risk (see the *Vigilance* section for details).

Study	Species	Stimuli	Predictions		
			Supported	Rejected	Not tested or controls lacking
Burger and Gochfeld (1998)	several waterbird spp.	people on foot	C		A, B, D
Duchesne et al. (2000)	woodland caribou	people on skis or snow shoes	C		A, B, D
Frid (2001*b*)	Dall's sheep	fixed-wing aircraft	A		B, C, D
Galicia and Baldassarre (1997)	American Flamingo	motorboat	C	B	A, D
Papouchis et al. (2001)	bighorn sheep	cars, bikes	C		A, B, D
Stockwell et al. (1991)	bighorn sheep	helicopter	A		B, C, D
Ward and Low (1997)	American Crow	urban pedestrians and traffic	B, D		A, C

Support for Prediction B was inconsistent (Table 2). Crows (*Corvus brachyrhynchos*) in urban environments were more vigilant and foraged less efficiently where disturbance stimuli were nearer (Ward and Low 1997), but American Flamingos (*Phoenicopterus ruber ruber*) were more vigilant when motorized tourboats were farther away (Galicia and Baldassarre 1997).

Several studies were consistent with Prediction C (Table 2). For instance,larger groups of people on foot had stronger effects on vigilance increases by both birds and ungulates (Burger and Gochfeld 1998, Duchesne et al. 2000).

Consistent with Prediction D, vigilance by crows following urban disturbance stimuli was affected by distance to obstructive cover and flock size (both positive relationships). Vigilance was also inversely related to distance to protective cover (Ward and Low 1997).

Habitat selection

Habitat choice is the outcome of decisions that balance the trade-off between predation risk and resource richness. Theoretically, animals should select habitats that minimize the ratio of mortality risk to net energy intake (Gilliam and Fraser 1987, reviews in Lima and Dill 1990, Lima 1998). Consistent with theory, individuals of taxa as diverse as fish (e.g., Gilliam and Fraser 1987), ungulates (e.g., Edwards 1983, Berger 1991), and small mammals (Morris and Davidson 2000) spend less time in places where richer resources are associated with greater danger. Whether animals under risk shift their habitats depends on the relative costs and benefits of leaving their current site and going elsewhere. Such decisions may be constrained by the species' perceptual range, the distance from which individuals can perceive key landscape elements (Lima and Zollner 1996, Zollner and Lima 1997).

Gill et al. (2001) use a predation risk framework to argue that animals that do not shift habitats when exposed to disturbance stimuli might have no suitable alternative habitats. Thus, animals are still impacted by being forced to remain at disturbed sites where the increased energetic costs of antipredator behavior reduce effective habitat quality.

Predictions regarding habitat selection, which have been proposed previously by disturbance studies grounded in predation risk theory, include the following. (A) Long-term, intense disturbance stimuli will cause habitat shifts (or observed avoidance of disturbed habitats when pre-treatment data are not available) at the cost of reduced access to resources. A different form of the prediction is that animals will access resources in habitats previously affected by disturbance stimuli once the latter are removed (Madsen 1994, 1998, Gill et al. 1996, Gill and Sutherland 2000). (B) Habitat shifts will not occur if alternative habitats are too distant or of low quality, such that the net benefits of shifting habitats do not outweigh the costs of remaining at disturbed sites (Gill et al. 2001).

Almost all of the reviewed studies strongly supported Prediction A, implying that alternative habitats were available in those systems (Gill et al. 2001). The pygmy marmoset (*Cebuella pygmaea*), a neotropical primate, shifted to the upper canopy in areas disturbed by ecotourists on foot and motorboats, but used the lower strata (which it normally prefers) in less disturbed areas (de la Torre et al. 2000). Available habitat and access to food were substantially reduced for disturbed Pink-footed Geese (*Anser brachyrhynchus;* Gill et al. 1996). For woodland caribou (*Rangifer tarandus caribou*) during late winter, functional habitat loss caused by avoidance of roads and other developments amounted to 48% of a 6000-km^2 study area (Dyer et al. 2001). Bottlenose dolphins (*Tursiops truncatus*) avoided important foraging areas when motorboat traffic was high (Allen and Read 2000). Table 3 summarizes these and additional examples. Such habitat shifts probably increase the strength of density-dependent processes (e.g., intraspecific competition) that affect demography (Gill and Sutherland 2000).

In contradiction to Prediction A, woodland caribou shifted habitats in response to wolves (*Canis lupus*), but not in response to people on skis and snowshoes (they did suffer costs to foraging and resting: Duchesne et al. 2000). Alternative habitat may have been of low quality and not worth shifting to without a very high risk of wolf predation. Unfortunately, Prediction B was not tested.

Consistent with Prediction B, diving ducks (mainly *Aythya* spp.) at a bay on Lake Erie fled from motorboats and promptly returned to the bay during spring, but during fall often redistributed into the adjacent and very large main lake. Spring was correlated with harsher conditions and partial ice cover on Lake Erie, which probably reduced the benefits of shifting habitats.

In contrast, the lake was suitable alternative habitat during fall, when habitat shifts did occur (Knapton et al. 2000). Similarly, Florida manatees (*Trichechus manatus latirostris*) during winter continued to use a bay with thermal springs (an essential resource for avoiding hypothermia) and did not shift into colder waters outside the bay, regardless of very high levels of boat traffic. At a smaller spatial scale and consistent with Prediction A, they selected areas within the bay with the least boat traffic (Buckingham et al. 1999).

ACQUIRING MATES

Individuals of many taxa signal to attract mates or warn off intruders to their territories, but such advertisement can attract predators (see reviews in Lima and Dill 1990, Magnhagen 1991, Lima 1998). Male Tungara frogs (*Physalaemus pustulosus*) are a classic example because their chorusing attracts both potential mates and predatory bats (*Trachops cirrhosus*). Frog responses to a model bat flying above their pond ranged from silencing mating calls but remaining on the pond's surface, to abandoning the site by diving (stronger responses corresponded to more direct approaches). The cost of safety was postponed access to mates (Ryan 1985).

Disturbance stimuli may cause similar trade-offs. Passerine birds sing to defend territories or attract mates; Gutzwiller et al. (1994) reported that some species (but not all) reduced their singing activity when humans walked through or near their territories. Relative to areas with little disturbance, pygmy marmosets in areas used intensely by ecotourists (on foot and in motorboats) had a lower frequency of trills, a display that serves to maintain contact with social groups and that might affect mate acquisition (de la Torre et al. 2000).

Table 3. Literature examples for assessing predictions concerning habitat shifts. Predictions (in shortened form; see text for more detail) were (A) long-term, intense disturbance stimuli will cause habitat shifts at the cost of reduced access to resources, but (B) habitat shifts will not occur if alternative habitats are unavailable or unsuitable. Unless both treatments are addressed, support for Prediction A makes Prediction B inapplicable. (See *Habitat selection*.)

Study	Species	Stimuli	Predictions		
			Supported	Rejected	Not tested or controls lacking
Allen and Read (2000)	bottlenose dolphin	motorboats	A		
Buckingham et al. (1999)	Florida manatee	motor and paddle boats	A, B		
de la Torre et al. (2000)	pygmy marmoset	people on foot and boats	A		
Duchesne et al. (2000)	woodland caribou	people on skis or snow-shoes		A	B
Dyer et al. (2001)	woodland caribou	roads, other linear developments	A		
Gill et al. (1996)	Pink-footed Geese	roads, vehicular traffic, related activities	A		
Knapton et al. (2000)	diving ducks	motorboats	A, B		
Lafferty (2001)	Snowy Plover	people on foot	A		
Lord et al. (1997)	New Zealand Dotterel[a]	people on foot	A		
Mace et al. (1996)	grizzly bear	roads, vehicular traffic, related activities	A		
Madsen (1998)	waterfowl (quarry and non-quarry species)	hunting activities	A		
Nellemann and Cameron (1998)	barren-ground caribou	road density and associated activities	A		
Nellemann et al. (2000, 2001), Vistness and Nellemann (2001)	reindeer[b]	road traffic; centers of human activity	A		
Papouchis et al. (2001)	Bighorn sheep	road traffic	A		

[a] *Charadrius obscurus aquilonius.*
[b] *Rangifer t. tarandus.*

For some lekking species, such as the Great Snipe (*Gallinago media*), both disturbance stimuli and predation risk can cause males to flee from a lek. These males must then choose between returning to the lek at the risk of re-encountering the predator, or losing access to females by continuing to hide. Males with a high mating probability are more likely to risk returning sooner (Kålås et al. 1995). Yet consider the likely case of an ecotourist who, after disrupting a lek, remains in place determined for another photograph, forcing lek members to hide longer and precluding matings for that period.

The potential impact of ecotourism on the reproductive success of lekking ungulates was discussed almost 30 years ago by McTaggart-Cowan (1974). Walther (1969) also warned that female Thomson's gazelles, whose flight initiation distance from a car is greater than that of males, would be unable to access male territories found within areas frequented by ecotourists. Although data are lacking, it is likely that human divers intent on photographing or viewing reef fishes often disrupt mating by displacing fish from their territories.

PARENTAL INVESTMENT

Predation risk can impact reproduction via decisions about parental investment. When predators threaten both offspring and the parent, should the parent defend the young and face potential death, or should it flee and expect future reproduction to outweigh the loss of current offspring? The decision depends on the parent's residual reproductive value. Parents of iteroparous species that produce few young per year but have long reproductive life-spans should be more likely to save themselves and abandon their current offspring, thus maintaining options for future reproduction (reviews in Clutton-Brock and Godfray 1991, Magnhagen 1991).

Disturbance stimuli may create similar trade-offs. If parents chose to desert young, however, offspring mortality may result from physical factors (e.g., cold temperatures) or facilitation of real predators, and not directly from the disturbance stimuli that threatened the parent. For example, during helicopter disturbance, a Dall's sheep lamb straying behind its fleeing mother fell prey to a Golden Eagle (*Aquila chrysaetos;* Nette et al. 1984). Many bird studies found that nestling predation increased when parents disturbed by humans abandoned the nest (e.g., Tremblay and Ellison 1979, Anderson 1988, Piatt et al. 1990). Further support is found in the lower survival rates of mountain goat (*Oreamnos americanus*) kids separated from their mother during disturbance events (caused by helicopter overflights or all-terrain vehicles) or during encounters with grizzly bears (*Ursus arctos;* Côté and Beaudoin 1997).

When a predator threatens offspring but not the parent, the parent may face a trade-off between energy gain and offspring protection. For Seychelles Warblers (*Foudia sechellarum*), nest guarding by males brings a seven-fold reduction in the rate of egg losses to predation, but time spent nest guarding is time not spent provisioning young or self-feeding. Such trade-offs may not only cause current offspring to starve, but also impact the parents' body condition and future reproduction (Komdeur and Kats 1999).

Parental investment theory should guide predictions of when disturbance stimuli will cause parent—offspring separation, thereby indirectly increasing predation rates on young (see Ghalambor and Martin 2000). Consider female bears (*U. arctos, U. maritimus,* and *U. americanus*) with vulnerable offspring hibernating inside dens. Costs of den abandonment can be high (one study reports a 10-fold increase in cub mortality) and a variety of disturbance stimuli, including seismic blasts, may cause den abandonment. Responses of individual mothers, however, are variable (review in Linnell et al. 2000). Could the probability of den abandonment be predicted in terms of the mother's residual reproductive value?

Although Clark and Ydenberg (1990) provide a framework for quantitative predictions, some qualitative predictions derived from parental investment theory are as follows: (A) When disturbance stimuli are very strong (e.g., direct approaches by helicopters, nearby seismic blasts) and vulnerable young cannot flee, parents with high residual reproductive value will be more likely to desert their young than parents that have already fulfilled most of their reproductive potential. (B) When young are not abandoned and disturbed parents increase their vigilance, hiding, or protection of young, parents with low residual reproductive value will compromise provisioning less than self-feeding, while parents with high residual reproductive value will do the opposite.

We did not find studies that could evaluate these predictions beyond indicating that disturbance does alter provisioning and self-feeding rates. Bald Eagles disturbed by campers increased the time spent protecting nestlings; consequently, the amount of prey consumed during provisioning and self-feeding dropped by almost one-third (Steidl and Anthony 2000). Mexican Spotted Owls decreased prey delivery rates after disturbance from helicopters and chainsaw-related noise, and the effect was stronger when stimuli approached more closely (Delaney et al. 1999). European Oystercatchers (*Haematopus ostralegus*) decreased the time spent incubating eggs, self-feeding, and provisioning young when disturbed by people on foot (Verhulst et al. 2001). Testing the effects of residual reproductive value is more difficult and would require studies of marked individuals of known ages.

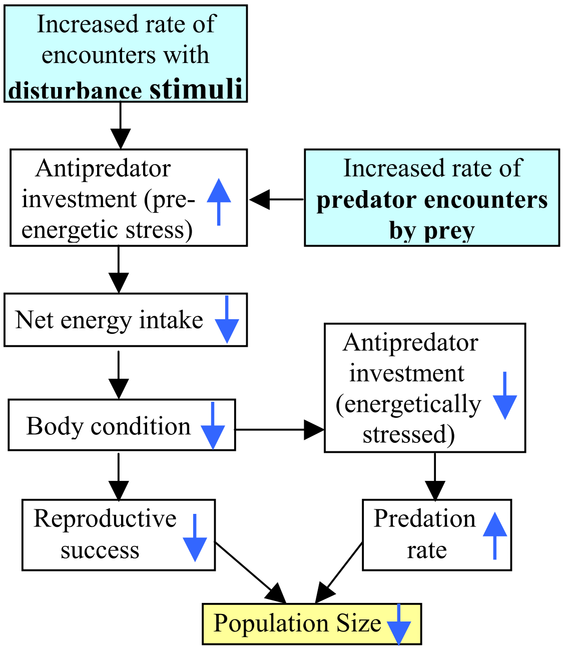
INDIRECT EFFECTS ON POPULATIONS

High levels of predation risk may indirectly affect survival and reproduction by causing prey to divert a large proportion of time and energy away from resource acquisition, so that body condition deteriorates and survival and reproductive success are reduced (Hik 1995, review in Lima 1998, Morris and Davidson 2000). Furthermore, as proposed by the Predation-Sensitive Foraging Hypothesis (Sinclair and Arcese 1995), animals in poor condition may experience greater predation rates when trying to avoid starvation by searching for additional food in dangerous habitats (McNamara and Houston 1987, Hik 1995, Sinclair and Arcese 1995, Sweitzer 1996).

Although only predation causes direct mortality, both predation risk and disturbance stimuli potentially affect population dynamics indirectly by altering an individual’s investment in antipredator behavior (reviews in Lima 1998, Gill and Sutherland 2000). If the response includes shifting habitats, then animals displaced from disturbed sites may experience greater intraspecific competition when forced to spend more time in suboptimal habitats, or when crowding into the small areas of good habitat that remain undisturbed (Gill and Sutherland 2000). In some systems, such redistribution in response to disturbance stimuli might also enhance the hunting success of real predators (Kilgo et al. 1998; but see Brown et al. 1999 and next section).

As outlined in Fig. 1, the risk-disturbance hypothesis predicts that long-term and intense disturbance stimuli can cause population declines via reduced body condition and consequent reductions in reproductive success, particularly during periods of high environmental stress (White 1983, Madsen 1994). Reduced body condition caused by high disturbance levels could also contribute to increased predation rates (Fig. 1; see Sinclair and Arcese 1995).

Fig. 1. Conceptual model outlining the behavioral mechanisms by which increased rates of human disturbance or of predator encounters by prey could cause population size to decline. Downward-facing arrows inside boxes indicate a negative response and upward-facing arrows indicate a positive response.



Observations of Pink-footed Geese are consistent with this prediction. Individuals in undisturbed areas gained body mass and had a breeding success of 46%. In contrast, individuals in areas where farmers consistently scared them off their fields did not gain mass and had a breeding success of 17% (Madsen 1994).

Ungulate studies provide further evidence of indirect disturbance effects on populations. The reproductive success of mule deer (*Odocoileus hemionus*) experimentally disturbed by an all-terrain vehicle (Yarmoloy et al. 1988) and of caribou disturbed by low-elevation jet flights (Harrington and Veitch 1992) decreased as disturbance rates increased. For elk (*Cervus elaphus*) disturbed experimentally by people on foot, the ratio of young to mothers was inversely related to disturbance rate (Phillips and Alldredge 2000). These studies did not address the underlying behavioral mechanisms, but were qualitatively consistent with energetic models of the behavioral

responses and reproduction of caribou disturbed by seismic exploration blasts (Bradshaw et al. 1998) and low-elevation military jet-fights (Luick et al. 1996).
Correlational evidence corroborates the experimental studies. Body mass and population size of barren ground caribou (*R. tarandus*) decreased as rates of military jet overflights increased (Maier 1996). The reproductive success of mountain goats correlated negatively with the cumulative number of seismic exploration lines placed two years prior to the birthing season (each kilometer of seismic line represented 6—8 km of helicopter flying and 22 person-days of ground work; Joslin 1986).

A study of grizzly bears foraging on army cutworm moths (*Euxoa auxiliaris*) provides additional support (White et al. 1999). When disturbed by hikers, bears reduced their energy intake by an average of 12 kcal/min (50.2 x 10^3kJ/min), and spent energy fleeing or acting aggressively toward hikers. The body condition and reproductive success of bears are likely to deteriorate if such reductions of net energy gain are long-term and cumulative (White et al. 1999). Similar examples exist for Snow Geese (*Chen caerulescens atlantica;* Bélanger and Bédard 1990).

Proper tests of reproductive impacts often will be difficult for large vertebrates, because it is often logistically not feasible to reach the large sample sizes required for adequate statistical power (e.g., Delaney et al. 1999).

INDIRECT EFFECTS ON COMMUNITIES

Facilitating predation by natural predators on vulnerable young is one way in which disturbance stimuli might negatively impact one trophic level while having a positive effect on another (see *Parental Investment*). Other community-level effects derive from predation risk affecting the distribution of foragers and, consequently, the foragers' influence on the density of their own prey. For example, when animals spend less time foraging in risky places, they consume a lower proportion of available resources in the area (e.g., Milinski 1985, Morris and Davidson 2000), which could have cascading effects at lower trophic levels (e.g., Chase 1998). Similarly, herbivores may consume a lower proportion of the plant biomass available in the vicinity of a disturbance center (e.g., roads; Gill et al. 1996, Nellemann et al. 2001, Vistness and Nellemann 2001). Thus, human activities can indirectly affect plant community structure by influencing the distribution and intensity of herbivory.

Community effects could also become manifest when 'fear' depletes a prey patch. For example, when two predators share a common prey, the hunting activities of Predator A might increase prey wariness (e.g., forcing it to spend more time in a refuge, increasing aggregation), thereby lowering the foraging success of Predator B (Crowder et al. 1997, Sih et al. 1998, Brown et al. 1999). In the case of disturbance, an analogous situation might arise when fish schools dive deeper to evade motorized vessels (e.g., Gerlotto and Fréon 1992), forcing aquatic predators that breathe air (e.g., cetaceans and seabirds) to increase their foraging costs through deeper dives.

Kilgo et al. (1998) hypothesize that human disturbance might facilitate predation by Florida panthers (*Felis concolor coryi*) on white-tailed deer (*Odocoileus virginianus*). The deer respond to hunting activities by shifting away from roads and open habitats and by increasing their nocturnal activity, which might increase their encounter rates with panthers (Kilgo et al. 1998). However, the predation rate might not necessarily increase with encounter rate (see Lima and Dill 1990, Abrams 1993). At least until the risk of starvation becomes high (Sinclair and Arcese 1995; see Fig. 1), deer can invoke an enhanced state of alertness (e.g., higher vigilance levels, larger and tighter groups) that might counteract increases in encounter rates. It is plausible that deer hunting activities could, in fact, decrease the hunting success of panthers (see Brown et al. 1999).

WHY INVOKE THE RISK-DISTURBANCE HYPOTHESIS?

Hundreds of useful and analytically sophisticated studies already address the effects of disturbance stimuli on animals without invoking the risk-disturbance hypothesis, or indeed any other theoretical framework, and many of them test predictions similar to those discussed here. So what is gained by formalizing and applying the risk-disturbance hypothesis? Although in some cases little might be gained, we argue that the hypothesis often will enhance a study's design and conservation value.

Some predictions regarding fleeing and vigilance are intuitive, and many studies address them at some level, although usually without formalizing them (Tables 1 and 2). Two types of predictions, however, are unlikely to be made a priori without a predation risk framework. First, there appear to be few studies that test how factors related to natural predation risk combine with the characteristics of disturbance stimuli (Prediction D in Tables 1 and 2). Although such predictions may not be relevant to all systems, not testing them will limit the explanatory power of some analyses. Second, it also appears rare for disturbance studies to consider how fleeing responses are affected by resource distribution or by environmental factors that affect locomotion costs (Prediction F of Table 1); none of the studies we reviewed did so a priori. Not considering this prediction may result in a large proportion of unexplained variability and may limit interpretation of the energetic costs of a given disturbance (see Ydenberg and Dill 1986).

In the case of habitat selection, the risk-disturbance hypothesis is not necessary for the intuitive prediction that disturbed animals will shift habitats when aversive disturbance is long term. A predation risk framework is more likely to provide an explicit focus for quantifying lost access to resources, but still is not essential (Table 3). The main issue arises when lack of habitat shifts is interpreted as no disturbance impact. As Gill et al. (2001) argued, there is a danger here of compromising the conservation implications of a study; animals that do not shift habitats simply may have no alternative place worth going to. If forced to remain in the disturbed habitat, their activity budgets probably will be disrupted.

In the case of mate acquisition and parental investment, studies not grounded on predation risk and life-history theory are unlikely to explain mechanisms behind interspecific differences in how disturbance stimuli affect mating displays, or why there is individual variability in how disturbance stimuli affects parental care. Not surprisingly, we found few data to assess our predictions.

Several studies did not need predation risk theory to make notable advances toward predicting and quantifying disturbance effects on population dynamics. We suggest that the risk-disturbance hypothesis, however, would increase the scope of models by ensuring that underlying mechanisms are considered a priori. In particular, none of the reviewed studies considered risk of starvation and predation-sensitive foraging (see Sinclair and Arcese 1995). In the case of community dynamics, the territory is wide open for disturbance studies, and a predation risk framework would be fruitful for guiding predictions. For instance, the model of Gill et al. (1996) could easily be modified to consider the perspective of the plant community, rather than of the herbivore. It was not surprising that we did not come across studies addressing how disturbance increases the baseline level of wariness of a prey species, and therefore indirectly reduces the hunting success of a predator that may be more tolerant of disturbance (see Brown et al. 1999).

At a very practical level, many disturbance studies begin by measuring myriad environmental and biological variables, and go through complex exploratory statistics to reduce the number of factors that would fit a parsimonious model. Clearly, a theoretical framework would focus predictions from the outset, streamline fieldwork and analyses, and increase the generality of results. We suggest that this approach would save time and money for conservation agencies because general predictions would shorten the path toward effective mitigation measures that do not over-regulate human activities.

Although we generally found that literature examples were consistent with predictions of the risk-disturbance hypothesis, some inconsistencies did arise, indicating that much stimulating work lies ahead for refining the concepts. We hope that our discussion stimulates a wider application of predation risk theory, as well as explicit tests of its predictions.

Responses to this article can be read online at: *http://www.consecol.org/Journal/vol6/iss1/art11/responses/index.html*.

Acknowledgments:

A. Frid was supported by a PGS-B scholarship from NSERC Canada. L. M. Dill's research is supported by NSERC Canada grant A6869. We thank Bernie Crespi, Ian Hamilton, and anonymous reviewers for critiquing earlier drafts. We also thank Darren Witt for producing the loom visualization.

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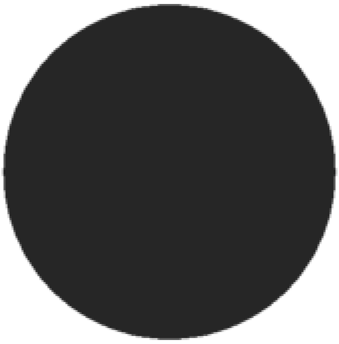
Appendix 1. An example of a generalized fright stimulus. Many animals initiate flight when the rate of change of angle subtended by an approaching object ("loom") exceeds some threshold. To repeat the animation, please refresh your browser or click the image. (For pdf version readers: Go to http://www.consecol.org/Journal/vol6/iss1/art11/appendix1.html to view this animated image)



BIOLOGICAL CONSERVATION 136 (2007) 232–245

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Return to the wild: Translocation as a tool in conservation of the Desert Tortoise (*Gopherus agassizii*) ☆

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ARTICLE INFO

Article history:
Received 31 May 2006
Received in revised form
16 November 2006
Accepted 27 November 2006
Available online 11 January 2007

Keywords:
Augmentation
Chelonian
Mojave Desert
Nevada
Relocation
Supplementation

ABSTRACT

Translocation could be used as a tool in conservation of the threatened Mojave Desert Tortoise (*Gopherus agassizii*) by moving individuals from harm's way and into areas where they could contribute to conservation of the species. Numerous factors may affect the success of translocations, including the conditions experienced by tortoises in holding facilities while awaiting translocation. The tortoises available for our translocation study had been provided supplemental water during their years spent in a captive holding facility, potentially inducing carelessness in water conservation. In addition to generally investigating the efficacy of translocation, we compared the effects of continuing with the effects of ceasing the holding facility's water supplementation regimen. After exposure to one of the two water regimens, all tortoises were given the opportunity to hydrate immediately prior to release. We examined behavior, body mass, carapace length, movement, and mortality of tortoises for two activity seasons following release to the wild. Water supplementation was correlated with high rates of carapace growth and distant movements by males after release. Lengthy movements following translocation may be problematic for conservation planning, but this should be evaluated in light of the goals and circumstances of each translocation project. Although the mortality rate was 21.4% in 1997, data suggest that drought conditions at the site rather than the translocation itself negatively affected the tortoises. None of the tortoises died during their second season at the site. Our results indicate that translocation should be considered a useful tool in conservation of the Desert Tortoise.

1. Introduction

Translocations of animals or intentional releases to the wild as attempts to establish, reestablish, or augment populations (Griffith et al., 1989) have been used with a number of species with varying levels of success. One review of translocation programs for reptiles and amphibians reported that only 19% were successful (Dodd and Seigel, 1991). Success rates may be higher, however, when programs of indeterminate success are eliminated from the calculation (Burke, 1991).

☆ Information on obtaining unpublished reports and documents cited in this paper may be requested by contacting the US Fish and Wildlife Service's Desert Tortoise Recovery Office in Reno, NV, USA.

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0006-3207/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2006.11.022

Definitions of success are variable and determining ultimate success can require lengthy studies (Fischer and Lindenmayer, 2000; Seigel and Dodd, 2002). Translocation may be a useful tool in conservation of some species, yet well designed studies are necessary to properly evaluate its efficacy.

The Mojave population of the Desert Tortoise (*Gopherus agassizii*) that occurs north and west of the Colorado River in the United States is protected as a threatened species under the federal Endangered Species Act (USFWS, 1990). The recovery plan associated with this federal listing included guidelines for experimental translocations (USFWS, 1994). In Las Vegas, Nevada, many Desert Tortoises were maintained in captivity at the Desert Tortoise Conservation Center (DTCC) after their removal from land undergoing urban development. We viewed experimental translocations as opportunities to test whether tortoises otherwise destined for lifetimes in captivity could be used to contribute to the recovery of the species. Some biologists have cautioned against releasing formerly captive animals because they may represent sources of disease, stress, and/or unplanned gene flow to wild tortoise populations (Berry, 1972, 1975; St. Amant and Hoover, 1978; Berry, 1986; Bury et al., 1988; Dodd and Seigel, 1991; Jacobson et al., 1991). Previous translocation studies suggested that formerly captive Desert Tortoises may not be competent in foraging or finding suitable shelter in the wild and short-term survival rates ranged from 0% to 100% for various cohorts (Berry, 1974; Cook et al., 1978; Cook, 1983). These studies did not provide sufficient evidence to support or contest the efficacy of translocation as a tool in conservation of the Desert Tortoise.

Captive and free-ranging Desert Tortoises differ considerably in their access to and use of water. Infrequent and unpredictable rainfall in the Mojave Desert allows wild tortoises few opportunities to drink, whereas tortoises at the DTCC receive provisions of water daily throughout their active seasons. Tortoises at the DTCC anticipate activation of the sprinklers and drink frequently (Ruby et al., 1994; Charles LaBar, personal communication). In addition, captive tortoises may not drink after rainstorms (Minnich, 1977) and some frequently void dilute urine (Robert Espinoza, personal communication). Retention of bladder water is important in that it can be reabsorbed for regulation of bodily solute levels (Dantzler and Schmidt-Nielson, 1966; Minnich, 1977) and hydration of dry plant matter in the gut (Peterson, 1996b). Captive tortoises conditioned to plentiful drinking water and no need to be conservative in retaining bladder water may experience functional drought conditions upon release to the wild. Although Desert Tortoises are able to cope with temporary imbalances in water budget (Nagy and Medica, 1986; Peterson, 1996a), tolerate high plasma osmolalities (Dantzler and Schmidt-Nielson, 1966; Minnich, 1977; Peterson, 1996a), and have low rates of water loss (Schmidt-Nielsen and Bentley, 1966; Naegle, 1976; Tracy, 1982; Nagy and Medica, 1986; Peterson, 1996a), mortality or morbidity caused by dehydration can be prevalent in drought years. During a drought in 1990, eight of nine deaths among a sample of 22 tortoises monitored in California were attributed to dehydration and related starvation (Peterson, 1994). We were concerned that the tortoises at the DTCC may have become too negligent about water conservation to do well in the wild, and we were interested in testing the effects of discontinuing water supplementation prior to release. In this study, we generally investigated the efficacy of translocation and tested the hypothesis that ending the supplementation of water in the fall prior to the spring release would increase initial success in translocation as measured through changes in body mass, changes in carapace length, behavior, movements, and mortality of translocated tortoises. This initial period began at time of release in spring and went up to the second period of winter inactivity following release. We refer to the periods of activity between hibernation events as activity seasons, thus from release to first hibernation is the first season and from end of first hibernation through beginning of second hibernation is the second season in the wild.

2. Materials and methods

2.1. *Study subjects*

We used 32 adult Desert Tortoises that had been maintained in outdoor pens at the DTCC for 7 yr and 10 juveniles that had been at the DTCC for 2 yr. All experimental tortoises were classified as negative on ELISA tests for antibodies to *Mycoplasma* spp. This reduced the chances of translocating tortoises infected with the pathogen *Mycoplasma agassizii*, which has been implicated as a cause of Upper Respiratory Tract Disease (URTD) (Brown et al., 1994). At the DTCC, tortoises received water daily throughout their active seasons until they entered hibernacula in fall 1996. Tortoises were removed from their pens on 25 and 26 March 1997, before many individuals had emerged from hibernacula and prior to the time that water was provisioned for that season. Adult experimental tortoises were 200–274 mm in carapace length with body masses of 1308–3401 g. Juvenile carapace lengths were 125–165 mm and body masses 334–603 g. On 27 March, the experimental tortoises were given the opportunity to drink for 30 min. After their body masses were recorded (Acculab Z6000 electronic balance), tortoises were placed in burrows inside randomly assigned experimental pens. Four males, four females, and two or three juveniles were released into each pen. Minimum time spent in the pens under experimental conditions was 27 days with some tortoises remaining in pens to up to 57 days. Each tortoise was fitted with a radio transmitter (AVM models G3, SB2, or SB2-RL for adults; SM1-H for juveniles) and was marked by notching the marginal scutes (Cagle, 1939) and by attaching a small numbered tag (of paper) to the carapace with epoxy. Transmitter attachment added <5% to the body mass of any animal.

2.2. *Experimental pens*

Tortoises were housed in four pens (15.2 m × 15.2 m) as the precondition before translocation. The pens had fiberglass walls (0.8 m) and water sprinklers. Two pens received water daily from 07:45 to 08:00 h (local time) beginning 28 March 1997. Three terracotta saucers were placed beneath the sprinkler's spray to collect water for the tortoises to drink. Tortoises from these pens are referred to as water-supplemented (WS). Two pens received no water, and those tortoises are referred to as not supplemented (NS). In each pen, three artificial burrows were constructed of polyvinyl chloride (PVC) pipes (1.22 m long and 38.1 cm diameter) cut in half lengthwise and buried at a downward angle in the soil. Two additional pieces of PVC pipe (30 cm diameter), cut in the same fashion as above, were laid on the ground as additional cover sites. The pens had comparable numbers of native shrubs. Tortoises ate dried alfalfa and slightly moistened iguana chow pellets (Zeigler Bros. Inc. 20% protein, 1/8 in. pellets, no. 53-6406-18-39) in keeping with the DTCC's feeding schedule.

2.3. *Translocation site*

The 90 km^2 translocation site, hereafter referred to as the Large-Scale Translocation Study (LSTS) site, was located in southern Nevada (WGS 84 Zone 11: 647,000 m E 3,953,000 m N). The north (bordered by Nevada Highway 161), south, and east (bordered by Interstate Highway 15) sides of the site had tortoise-proof fencing, and the unfenced western border was formed by the Spring Mountains. The resident, wild tortoise density was approximately 15–20 tortoises/km^2 (USFWS, unpublished) in a Mojave Desert scrub plant community dominated by the creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) association (Turner, 1982). Climate of the site was typical for the northeastern Mojave Desert with approximately 97 mm of annual precipitation (occurring in summer and winter) and temperatures ranging from the mean January minimum of −0.1 °C to the mean July maximum of 40.1 °C (Rowlands, 1995).

The release area was located approximately 32 km southwest of the DTCC. Tortoise density in the release area was likely depressed due to mortality by motor vehicles on Interstate Highway 15 prior to installation of fencing for this translocation project (Hoff and Marlow, 2002). We dug 13 burrows (0.3 m long, spaced 19–49 m apart) with a power auger and shovels in the central-eastern section of the LSTS site. We did not plan to release more than 6 tortoises a day (limited by observer availability), yet wanted enough burrows available in the event that some tortoises occupied these burrows subsequent to their days of release. Burrows were labeled with metal tags, and their Universal Transverse Mercator (UTM) coordinates were measured using a Global Positioning System (GPS) unit. These burrows served as the starting points of released tortoises.

An automated weather station and four rain gauges on site measured rainfall. Additional rainfall data were obtained from the Jean Airport (7 km from release area, <0.5 km from northeastern border of LSTS site) and McCarran International Airport (approximately 45 km northeast of the LSTS site).

2.4. *Release*

Tortoises were placed in plastic tubs and transported by truck to the LSTS site (48 km by road). So that water supplementation regimen (to address potential careless voiding of bladder water after release) would be a variable, rather than time since last drink, all tortoises were given access to about 3 cm of water in their tubs for 20 min prior to release. Body masses before and after this procedure as well as observations of drinking and/or voiding were recorded. Tortoises were released by placing them headfirst into burrows. Twenty-eight tortoises were released from 23 April to 23 May 1997. Releases took place between 08:00 and 09:57 h, when air temperatures ranged from 21.5 to 30.0 °C. Six females, eight males, and one juvenile from the WS group were released, while seven females, five males, and one juvenile from the NS group were released (Table 1). High ambient temperatures prevented releases 6–19 May and prohibited release of the remaining 14 tortoises.

Each tortoise's behavior was observed for approximately 4 h on the days of release. Observers recorded items ingested and marked the paths traveled by the tortoises with flagging, so that the actual distances moved by tortoises could be calculated.

2.5. *Body mass and carapace length*

Body masses were measured using a Pesola spring scale in 1997 and an Ohaus electronic balance (model CT 6000) in 1998. Straight-line carapace lengths were measured with slide calipers (Haglof Inc., Sweden). Body mass and carapace length were recorded on day of release, 15 days after release, and once a month thereafter.

2.6. *Animal movements*

Tortoises were located up to twice weekly using a handheld receiver (Telonics) and antenna through July in 1997, except when radio signals were lost temporarily. Tortoises were tracked once each month from August 1997 to April 1998 and once each week from May 1998 to November 1998. Data recorded each time a tortoise was located included UTM coordinates, descriptive location, behavior, and condition of the animal.

2.7. *Analyses*

Data were checked for homogeneity of variance using Brown–Forsythe tests and for normality using Kolmogorov–Smirnov tests. Analyses of covariance were used to analyze change in body mass of WS and NS tortoises while in experimental pens and on the day of release with body mass at time of placement into experimental pens as the covariate. Repeated measures analyses of variance (ANOVA) were used to analyze changes in body mass after day of release, with sex and treatment as factors, and tortoise movements, with sex by treatment group as a factor. Home range sizes were calculated and mapped in ArcView™ (ESRI, Redlands, CA, USA) with the animal movement extension (Hooge and Eichenlaub, 1997) using the minimum convex polygon method. Mean home range sizes were compared using ANOVA with sex by treatment group as a factor, followed by a comparison between the sexes. Mean rates of changes in carapace length were compared using ANOVA for tortoises that survived for the length of the study with year, sex, and treatment as factors. Rates of mortality for the sex by treatment groups were compared using Pearson's Chi-square and Fisher's Exact tests. Software used for calculations included StatView™ v.4.51 and

Table 1 – Summary of Desert Tortoises translocated and their changes in body mass on day of release before and after the opportunity to drink

Tortoise #	Sex	Experimental group	Date released (1997)	% Change in body mass	Observed to drink	Excreted urine or feces
L1002	F	NS	23 April	16.67	Yes	–
L1003	F	NS	23 April	0.00	No	–
L1001	J	NS	23 April	0.00	Yes	Feces
L1005	F	WS	23 April	0.00	No	Feces
L1004	J	WS	23 April	0.00	Yes	Feces
L1006	M	WS	23 April	0.00	No	Feces
L1025	F	NS	29 April	7.14	Yes	–
L1026	M	NS	29 April	25.00	Yes	Urine (very little)
L1024	M	WS	29 April	−3.26	Yes	Feces
L1023	M	WS	29 April	0.00	No	–
L1222	F	NS	05 May	14.66	Yes	–
L1223	M	NS	05 May	0.00	No	–
L1226	M	NS	05 May	26.56	Yes	–
L1224	F	WS	05 May	−0.06	No	Feces
L1225	F	WS	05 May	−2.13	No	Feces
L1294	F	NS	20 May	9.46	Yes	Urine
L1296	M	NS	20 May	5.63	Yes	–
L1297	M	NS	20 May	23.81	Yes	Urine
L1295	F	WS	20 May	1.89	Yes	–
L1299	F	WS	20 May	−4.74	No	Urine
L1298	M	WS	20 May	0.00	–	Feces
L1346	F	NS	21 May	15.00	Yes	–
L1347	F	NS	21 May	13.81	Yes	–
L1349	F	WS	21 May	1.19	No	–
L1348	M	WS	21 May	0.00	No	–
L1367	M	WS	22 May	2.27	Yes	Feces
L1368	M	WS	22 May	0.00	No	–
L1363	M	WS	23 May	1.38	No	–

No datum was recorded as to whether L1298 was seen drinking. Excretion of urine or feces occurred between the measurements of body mass.
F = female, J = juvenile (undetermined sex), M = male, WS = water-supplemented, NS = not supplemented.

SuperANOVA™ v.1.11 (Abacus Concepts Inc., Berkeley, CA, USA).

3. Results

3.1. Behavioral observations

On the days of release, all tortoises exited their initial burrows within 30 min and ate during the observation period. Tortoises primarily ate dry plants of the following species: *Schismus barbatus*, *Bromus madritensis* (*rubens*), *Plantago* sp., and *Erioneuron pulchellum*. *Chamaesyce albomarginata* and *Baileya multiradiata* were eaten green. Eight of 13 NS tortoises and 7 of 15 WS tortoises ate cacti (*Opuntia basilaris* and *Opuntia ramosissima*).

Half of the tortoises, seven from both the WS and NS groups, were observed digging on the days of release. Most of these animals did not construct complete burrows during the observation period. One male NS tortoise (L1296) successfully completed a burrow in a sandy wash in less than 1.2 h.

Only two tortoises showed obvious signs of stress on their day of release. A NS female (L1222) began frothing at the mouth at 12:45 h on 5 May 1997 and immediately started digging beneath a creosote bush. During the next hour of observation, she stopped frothing, walked to a previous location, began to froth again, and dug beneath another creosote bush where she stopped frothing and remained for the last hour of observation. A WS male (L1298) began frothing at 11:40 h on 20 May 1997, but details of his behavior are unknown. No tortoises showed signs of heat stress during observation periods after the day of release.

3.2. Body mass

Adult WS tortoises gained 14.2% (SD = 7.7) while NS tortoises lost 2.4% (SD = 4.4) ($F_{1,23} = 31.7$, $p = 0.0001$; regression coefficient = −0.012, $p = 0.0200$) of their body masses while in experimental pens before translocation. Natural drinking opportunities during the treatment period were non-existent to extremely limited as no precipitation was recorded at the DTCC in March and May and 1 mm was recorded in April. After access to water on the days of release, adult NS tortoises increased body mass by 13.2% (SD = 9.1), while WS tortoises lost 0.25% (SD = 1.9) ($F_{1,23} = 27.0$, $p = 0.0001$) (Table 1). Many WS tortoises voided feces or urine in the tubs of water. The NS tortoises gained more body mass during the opportunity to drink than they had lost while in the experimental pens (paired *t*-test: $t_{11} = -4.741$, $p = 0.0006$).

Most adult tortoises (24 of 26) lost body mass following their release into the LSTS site until rainfall began in July

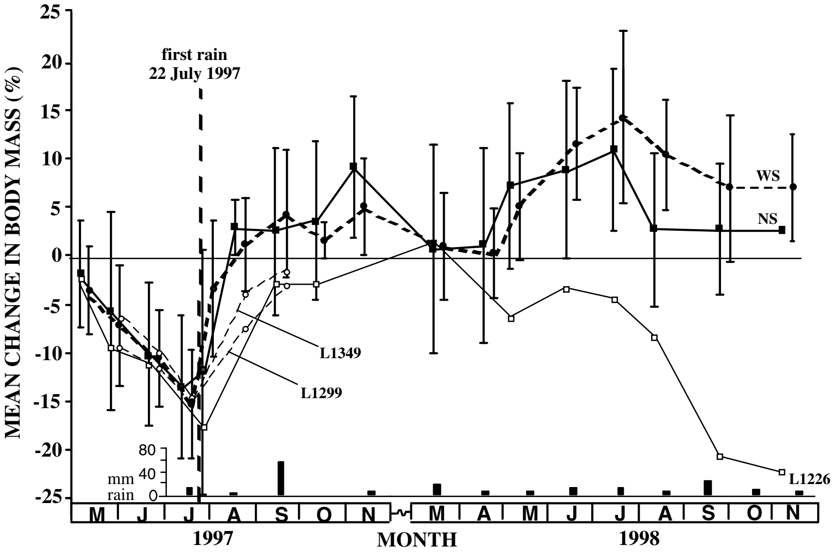


Fig. 1 – Mean change (%) in body mass (±1 SD) of WS and NS adult *G. agassizii* following release at the LSTS site. L1299, L1349, and L1226 were tortoises that showed signs of respiratory disease for >1 month and were not included in the group means.

1997. A single tortoise (L1367) voided small amounts of clear urine on three occasions (November and December 1997, January 1998) when handled. Changes in body mass were compared both by date (18 time periods), such that rain events would be reflected in changes in body mass of all tortoises during those time periods, and by number of days since release (four time periods). There were no significant relationships between initial body masses (potential covariate) and changes in body mass when examined by day since release or by date. Three tortoises (L1226, L1299, L1349) had visible signs of respiratory disease for extended periods of time and their changes in body mass were not included in the comparisons. Changes in body mass did not differ across repeated measures by date for the sexes ($F_{1,18} = 0.229$, $p = 0.6378$), treatments ($F_{1,18} = 0.123$, $p = 0.7300$), or the sex by treatment interaction ($F_{1,18} = 0.552$, $p = 0.4670$). In addition, WS and NS tortoises did not differ within time periods examined ($F_{16,142} = 1.009$, $p = 0.4507$) (Fig. 1). When controlling for number of days since release, groups of males and females with and without supplemental water (sex by treatment interaction) did not have different changes in body mass across all days ($F_{1,18} = 0.379$, $p = 0.5458$) or within the time periods ($F_{3,39} = 0.510$, $p = 0.6777$) (Fig. 2). Throughout 1998, groups that had been with or without supplemental water were heavier on average than they were on the days that they were released (Figs. 1 and 2).

3.3. *Carapace length*

Tortoises that survived the length of the study grew much more slowly in 1997 (0.001 mm/day, SD = 0.009) than they did in 1998 (0.026 mm/day, SD = 0.022) ($F_{1,26} = 12.696$, $p = 0.0014$). No significant effects were produced by sex ($F_{1,26} = 2.834$, $p = 0.1043$), treatment ($F_{1,26} = 0.437$, $p = 0.5143$), or any of the interactions. When data from 1997 and 1998 were pooled and a single rate of change in carapace length for each tortoise was calculated for the length of the study, adult WS tortoises grew significantly faster overall (0.014 mm/day, SD = 0.006), than did NS tortoises (0.007 mm/day, SD = 0.006) ($F_{1,15} = 6.230$, $p = 0.0247$). The data on five tortoises ended in September 1997, so we examined changes in carapace length for all tortoises through the end of August 1997. Interestingly, the tortoises shrank during this period by an average of 0.0145 mm/day (SD = 0.0195). Only the two juveniles and two of the adults had positive growth rates during this time.

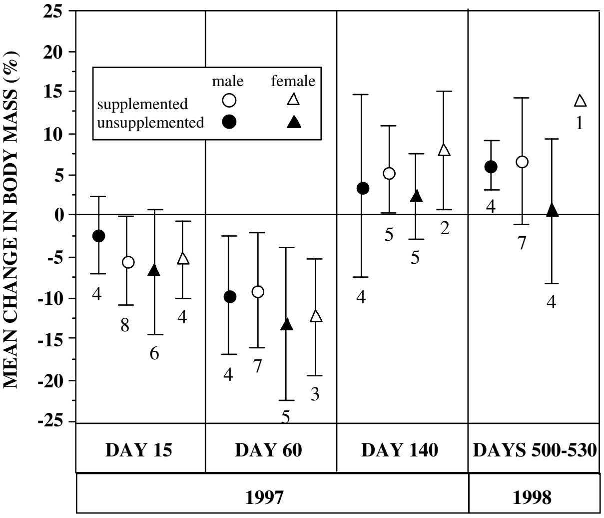


Fig. 2 – Mean change (%) in body mass (±1 SD) of adult *G. agassizii* from day of release. Sample sizes are given below each mean. Day 15 occurred from 7 May to 6 June, day 60 from 21 June to 20 July, day 140 from 9 September to 8 October, and days 500–530 from 29 September to 5 October. In 1998 measurements were recorded monthly, rather than for specific days since release.

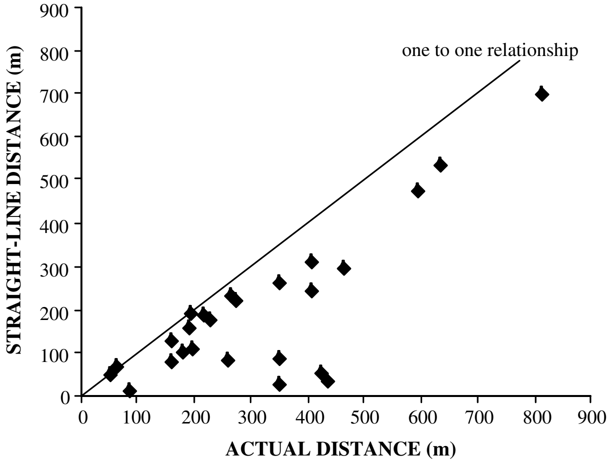


Fig. 3 – Straight-line and actual distances moved from initial burrow on day of release. The line represents a one to one relationship between the two metrics of distance moved. Tortoises with points close to the line traveled in nearly straight lines from their initial burrows. See text for discussion of tortoises that deviated from the line.

3.4. *Movement*

All but two tortoises moved away from their burrows on the days of their release. Movement patterns varied from nearly straight-line travel for many of the animals to meandering travel within the area of release (Fig. 3). There were no differences in actual or straight-line distances moved from initial burrows on days of release for the sexes (actual: $F_{1,19} = 0.010$, $p = 0.9225$; straight-line: $F_{1,19} = 0.206$, $p = 0.6551$), the treatments (actual: $F_{1,19} = 1.483$, $p = 0.2382$; straight-line: $F_{1,19} = 0.621$, $p = 0.4403$) or the sex by treatment interaction (actual: $F_{1,19} = 0.455$, $p = 0.5079$; straight-line $F_{1,19} = 0.326$, $p = 0.5750$). The amounts of time that the tortoises were observed moving were used as covariates (actual: regression coefficient = 0.773, $p = 0.0649$; straight-line: regression coefficient = 0.392, $p = 0.5917$).

The straight-line distances moved in 1997 by the groups were compared for six time periods. WS females were not included in the analysis because only one tortoise was not lost to mortality or transmitter failure at some point during the six time periods examined. The sex by treatment groups did differ ($F_{2,12} = 5.86$, $p = 0.0168$). Male WS tortoises moved significantly farther from the area of release than did NS males (Scheffe's S $p = 0.0172$) (Fig. 4a). Most of the movement away from the points of release occurred during the first 2 weeks following release. The tortoises did not show tendencies to orient northward toward the DTCC and the Las Vegas Valley (Fig. 5).

Total distances moved in 1997 also were compared by adding together the straight-line segments among locations (for the same periods of time that distance from point of release was calculated). Again WS females were not included in the overall analysis and the sex by treatment groups were different ($F_{2,12} = 4.48$, $p = 0.0352$) with WS males moving farther in total distance than NS males (Scheffe's S $p = 0.0383$). Approximately 20 weeks after release (one of the six time periods examined), total distance moved averaged 5845 m (SD = 2633) for WS males, 1872 m (SD = 1738) for WS females, 1781 (SD = 784) for NS males, and 3182 m (SD = 1950) for NS females. Total distances moved for animals with data points in the last period examined were not correlated with the number of relocation events ($R^2 = 0.052$, $F_{1,13} = 0.719$, $p = 0.4118$).

In their second season after release, tortoises remained much closer to their hibernacula than they had to their release burrows. The mean distance from hibernacula to areas of activity from May through September 1998 (11 time periods examined) was 275 m (95% CI ± 29.18) for all tortoises with no differences among the sex by treatment groups ($F_{2,11} = 0.370$, $p = 0.6991$) (Fig. 4b). Two WS males (L1298 and L1363) had movement patterns unlike those of the other tortoises (Fig. 4b). Their outlying points, as well as data from the single WS female were not included in the comparison.

Total distances moved in 1998 also were compared. Tortoises were located 21–38 times after emergence from hibernacula in 1998. The total distances moved and the number of relocation events between emergence from hibernacula and return to hibernacula were not correlated ($R^2 = 0.0004$, $F_{1,16} = 0.007$, $p = 0.9346$). Total distances moved did not differ for the sex by treatment groups ($F_{2,13} = 2.264$, $p = 0.1433$). Adult tortoises moved 5160 m (SD = 1633) in total distance during 1998.

3.4.1. *Use of burrows*

Tortoises used burrows as shelter sites during the study with no differences in the number of burrows used among the sex and treatment groups (sex: $F_{1,14} = 0.012$, $p = 0.9161$; treatment: $F_{1,14} = 0.933$, $p = 0.3506$; interaction: $F_{1,14} = 0.012$, $p = 0.9161$). Individuals tracked continuously through the end of 1997 used an average of six burrows (SD = 1.9, range = 3–10), and tortoises used eight burrows (SD = 2.6, range = 5–13) in 1998. On average, tortoises continued to use only one (SD = 0.87, range 0–3) burrow in 1998 that they first used in 1997.

Two tortoises returned to their initial human-made burrows. A WS female (L1295) was found in her initial burrow on the morning of 21 May 1997, 1 day after her release. The previous day this tortoise moved 439 m during the 3.5 h observation period (129 m straight-line distance). On 8 June 1998, a NS male (L1297) was found in the burrow within which it had been released on 20 May 1997. This tortoise was found up to 291 m from this burrow for all prior locations.

Many tortoises used their 1997–1998 hibernacula as shelter sites in 1998. Eleven of the 18 tortoises for which hibernacula were known returned to hibernacula after emergence. Two tortoises used the same burrows as both their 1997–1998 and 1998–1999 hibernacula.

3.4.2. *Home range*

Home ranges were calculated for adults in 1998 (Fig. 6), except for the two males (L1298 and L1363) that moved long distances in September 1998. Home range sizes did not differ for the sex by treatment groups ($F_{2,11} = 3.433$, $p = 0.0694$; single WS female not included) and males were not affected by treatment ($F_{1,8} = 1.225$, $p = 0.3006$). Because males and females typically have different home range sizes, data from treatment groups were combined and sexes were compared. The mean size of home ranges for male tortoises, 25.5 ha

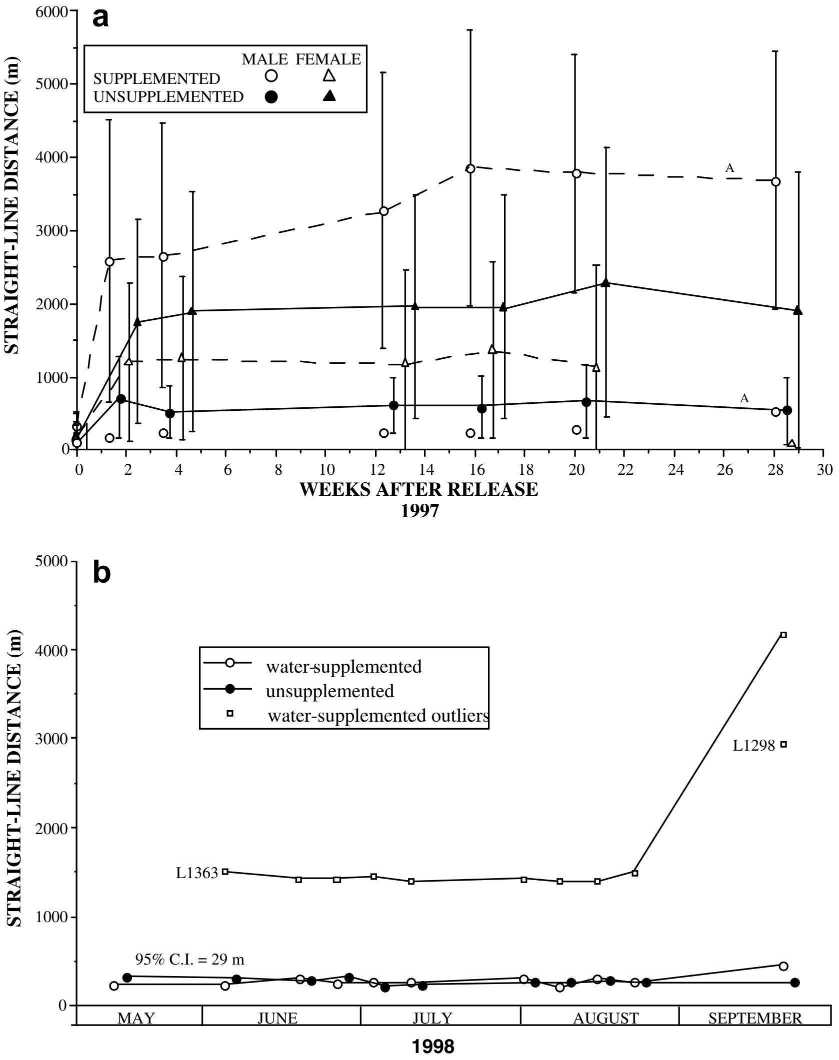


Fig. 4 – (a) Mean straight-line distances of *G. agassizii* from their initial burrows in 1997. Error bars represent one standard deviation. WS males moved significantly farther than did NS males (A). The open circles without connecting lines represent an outlier of the WS males (L1023). The open triangle without a connecting line represents a single WS female (L1005). (b) Mean straight-line distances from hibernacula of WS and NS adult *G. agassizii* in 1998. Two tortoises (L1363, L1298) had points that were outliers of the WS tortoises. WS and NS tortoises did not differ across all time periods $F_{1,15} = 0.053$, $p = 0.8209$, or within time periods $F_{10,139} = 1.310$, $p = 0.2309$.

(SD = 15.1, range = 9.94–62.73), was larger than that of females, 8.9 ha (SD = 1.9, range = 6.89–11.14) ($F_{1,13} = 5.804$, $p = 0.0315$). Tortoises located more times did not have larger home range sizes than those located fewer times (regression coefficient = −0.016, $p = 0.1914$).

3.5. *Mortality*

All six tortoise deaths occurred in 1997 (Appendix) giving a mortality rate of 21.4% (10.7% unknown outcome, 67.9% known survival) for tortoises from release to hibernation in 1997. Mortality rates were not significantly different for the main effects of sex (chi square = 3.467, df = 1, Fisher's Exact $p = 0.1602$), water treatment (chi square = 0.5159, df = 1, Fisher's Exact $p = 0.6546$), or among the sex by treatment groups (chi square = 4.573, df = 3, chi squared $p = 0.2059$).

The only adult male that died (L1348) had been supplemented with water. This animal had traveled as far as 1241 m from its initial burrow during the 48 days that it lived at the LSTS site. The tortoise had wet nares, a possible sign of disease, 1 week before its death. On 7 July 1997, the tortoise's intact carcass was found 1185 m from its initial burrow, and it had used four other burrows. There was no evidence that predation was the cause of death.

Two NS females died. L1002 was never found using a burrow between its release and death. This tortoise traveled long distances following release, and 21 days after release (13 May) its intact carcass was found overturned 4195 m from the initial burrow. L1025's carcass was found 166 days after release (11 October). The carcass was found soon after death at a location 5399 m from its initial burrow. The condition of the carcass and manner in which it was slightly buried and covered with grasses was consistent with predation by either bobcat (*Lynx rufus*) or mountain lion (*Felis concolor*).

Three WS females died. Females L1299 and L1225 were found with wet nares before their deaths and were preyed upon or scavenged. L1299's radio signal was last heard 117 days after release (13 September) and its carcass was located 18 February 1998. L1225 only used a single burrow up to its death 57 days after release (30 June). L1295 was found using one burrow until 91 days after release (18 August) when it was found dead in its second burrow. The burrow was located in a small wash and had collapsed, encasing the carcass in soil and cobble. The circumstances suggest that this tortoise remained in the burrow during a rainstorm and did not dig itself out when the burrow collapsed.

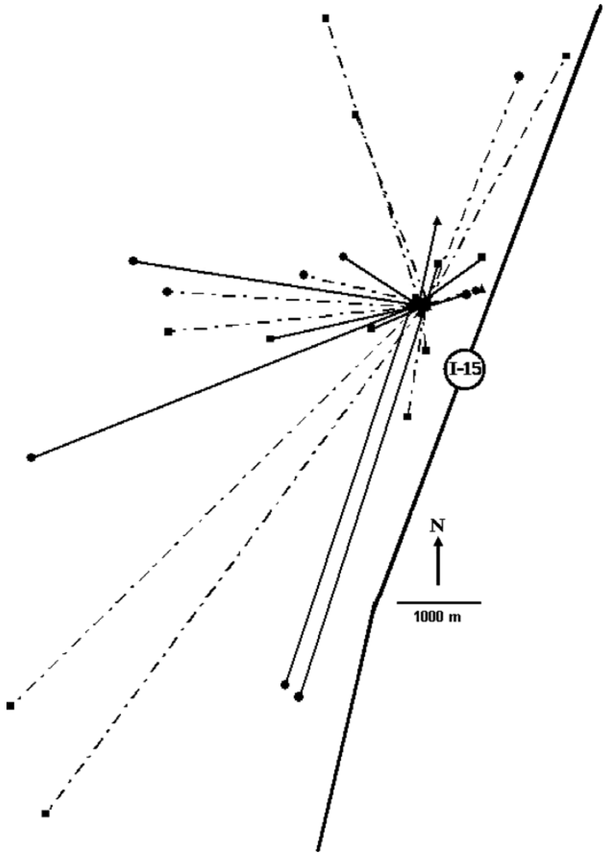


Fig. 5 – Straight lines from initial burrows to last known locations of all tortoises in 1997. Solid lines are NS, broken lines are WS, circles are females, squares are males, and triangles are juveniles.

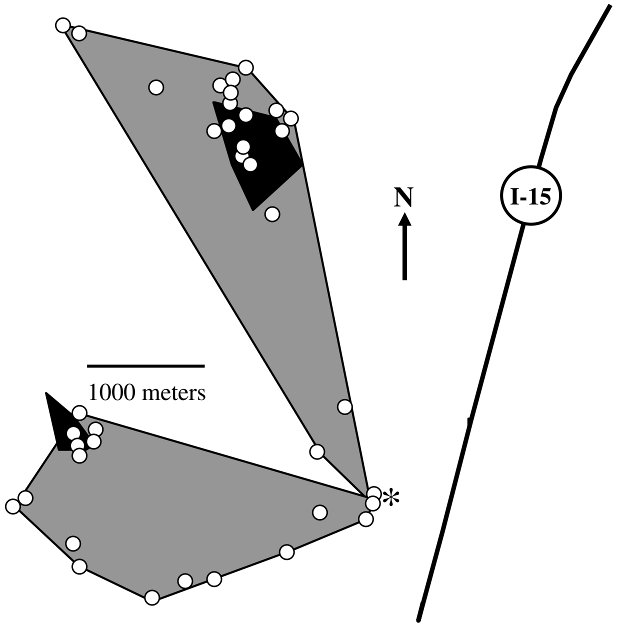


Fig. 6 – Movements by WS male L1006 (upper) and NS female L1222 (lower). 1997 locations (white dots) and minimum convex polygon home ranges for 1997 (grey) and 1998 (black) to show inappropriateness of calculating home ranges for first-season translocatees. * marks the release area. Interstate Highway 15 runs along the eastern border.

4. Discussion

4.1. *Behavioral observations*

Although the tortoises had spent years in captivity at the DTCC, upon release they were capable of finding appropriate food items, digging burrows, and generally using resources as necessary for survival in the wild. A previous translocation study raised concerns that released captives may have diminished ability to forage, find shelter sites, respond appropriately to environmental conditions, and avoid predators because all 5 tortoises died after translocation (Berry, 1974).

Overheating was shown to be a problem for tortoises in another translocation study with 6 of 7 deaths attributed to lethal body temperatures, three of which occurred on days of release (13 June and 2 July 1977) and three within 2 weeks of release (Cook et al., 1978; Cook, 1983). Tortoises that approach lethal body temperatures often produce large amounts of foaming saliva, which spread to the head and neck (McGinnis and Voigt, 1971). Two of our tortoises (L1222, L1298) were moving around the area of release and frothing at the mouth while all other tortoises released on those days were in shaded locations either at rest or digging beneath shrubs. During the observation periods both tortoises rested briefly in shade although they did not use shade competently as temperatures increased during the day. Both tortoises survived the length of the study, indicating that inappropriate thermoregulatory behaviors were likely limited a short period of time immediately following translocation. Problems associated with overheating would likely be minimized by conducting translocations in early to mid-spring, rather than late spring to summer, and by releasing tortoises such that on their first day they have several hours to move about when ambient temperatures are not likely to be problematic.

4.2. *Body mass*

Fluctuations in body mass of the Desert Tortoise largely are caused by changes in state of hydration (Minnich, 1977; Peterson, 1996a). When water is available, Desert Tortoises commonly drink 11–28% of their body mass (Minnich, 1977; Nagy and Medica, 1986), and in some cases, Desert Tortoises have been observed to increase body mass up to 43% after drinking (Miller, 1932).

Our concern that daily water supplementation in captivity could cause negligence in bladder water retention after release and our prediction that WS tortoises would lose more body mass after release than would NS tortoises were not supported by our data. Indeed, all tortoises lost similar amounts of body mass after release during the dry period preceding the first rain (22 July 1997). As expected, all tortoises gained body mass when rain provided drinking water. The two groups of tortoises continued to have similar fluctuations in body mass for the duration of the study.

Evaporative water loss is low in Desert Tortoises, but highly active animals lose more water through evaporation than do less active animals (Tracy, 1992). Desert Tortoises in California, at Ivanpah Valley (IV) and the Desert Tortoise Natural Area (DTNA), had a mean net water loss rate of <2 mL kg^{-1} day^{-1} (0.083 mg g^{-1} h^{-1}) during a severe drought; the typical rate was 1 mL kg^{-1} day^{-1} (0.042 mg g^{-1} h^{-1}) (Peterson, 1996a). Based on Peterson's observed rates, the tortoises at the LSTS site are predicted to lose 1.5–3.0% of their starting body masses after 15 days, but the actual body mass lost by LSTS tortoises was 5.3%. The LSTS tortoises are predicted (from Peterson's data) to drop 6.0–12.0% of their starting body masses after 60 days. The 10.8% (SD = 5.7) lost by LSTS tortoises is within the predicted range.

4.3. *Carapace length*

The fifth wettest year on record for southern Nevada (as measured in the Las Vegas Valley, approximately 45 km northwest of the LSTS site) occurred in 1998, with wettest ever February (73 mm) and tenth wettest March (26 mm) (Gorelow, 2005). February and March 1997 had below normal rainfall with 5 mm and 0 mm respectively. Late winter and early spring rains allow for germination and growth of the annual plants that make up much of the tortoise's diet (Oftedal, 2002). Tortoises translocated to the LSTS site grew about 25 times faster in carapace length during 1998 than they did during 1997. Shell growth positively correlates with rainfall (Medica et al., 1975; Nagy and Medica, 1986) and likely is dependent on nitrogen provided by green plants (Peterson, 1996b). Additionally, with drinking water available, tortoises can increase consumption of forage without elevating plasma solute concentrations to dangerous levels. The observed shrinking of carapace length from the time of release until the end of August 1997 helps to account for the large difference in growth rates for 1997 and 1998. During a tortoise's lifetime there are likely many periods when no growth or shrinking occurs. Adults and juveniles may experience no growth or shrinking during drought, yet in productive seasons juveniles may rapidly approach the size of more slowly growing older tortoises. Decrease in carapace length during drought was noted for two juvenile tortoises in another study (Berry et al., 2002) and shrinking has been measured in marine iguanas in times without food (Wikelski and Thom, 2000).

Carapace growth was marginally greater for tortoises that were supplemented with water although the small difference in growth rate was only detectable when the data from 1997 and 1998 were combined. The increase in size was not great enough to expect increased reproductive capabilities or decreased vulnerability to certain predators.

4.4. *Movement*

Familiarity with surroundings likely influenced the reduced movements made by tortoises in 1998 compared to those in 1997. We translocated a cohort of tortoises to the LSTS site in spring 1998 as part of another experiment. These tortoises moved an average of 1579 m (SD = 1071) from their initial burrows that year whereas tortoises released the year before moved only 275 m from their 1998 start points (hibernacula). The two cohorts were very similar vis-à-vis their movements in their first year after release suggesting that reduction of movement by tortoises in their second year was not simply caused by break of the drought, but by familiarity with the area.

The concept of home range was described and defined by Burt (1943) as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." Occasional movements to points outside of the area typically used should not be included in the home range and home ranges should not be calculated for animals that are wandering (Burt, 1943). The movement patterns of tortoises during their first season at the translocation site clearly were not consistent with the definition. Calculations of home ranges appeared to be appropriate for most animals in their second season after release. Desert Tortoises do make lengthy journeys outside of their normal activity areas to exploit resources such as calcium rich soils (Marlow and Tollestrup, 1982). Three tortoises that made long distance movements in 1998 did not return to their previous areas of activity, so home range calculations were inappropriate. Home range sizes of female (8.9 ha, range 6.9–11.1) and male (25.5 ha, range 9.9–62.7 ha) tortoises during their second activity season at the LSTS site were comparable to the home range sizes of native wild Desert Tortoises in a nearby valley in a non-drought year (females 5.9–11.2 ha, males 7.7–49.0 ha) (O'Connor et al., 1994). The characteristic home range sizes and the short distances moved from hibernacula provide evidence that second-year translocatees were similar to native wild tortoises from other studies.

Fidelity to the release site shown by some tortoises during their first and second seasons after release could, in part, be predicted by examining the patterns of movement on days of release. Six tortoises deviated greatly from straight-line travel and/or moved small straight-line distances from their initial burrows (Fig. 3). Two of these animals were frothing from the mouth. These two tortoises may have meandered because they became overheated, or the meandering may have been due to unfamiliarity with the surrounding area and misuse of shade resources. The other four tortoises (L1295, L1297, L1346, and L1005) were closer to their initial burrows ($\leqslant$110 m) at their last known locations in 1997 than were the other tortoises. The four tortoises represented each of the sex by treatment groups except for the WS males, who were already making long, linear movements away from their initial burrows. Three of the four tortoises survived through 1998 and were closest to their initial burrows at their last locations in 1998 as well (139–415 m) (Table 2). All other tortoises moved greater straight-line distances from their initial burrows of release and/or tended to move in nearly straight-lines from their

Table 2 – Straight-line distances moved by tortoises

Tortoise #	Sex	Experimental group	1997 Straight-line (m)	1998 Straight-line (m)	Final straight-line (m)
L1002	F	NS	4195 (21)*	–	–
L1003	F	NS	4314 (239)	65	4262
L1025	F	NS	3483 (139)*	–	–
L1222	F	NS	2433 (227)	290	2706
L1294	F	NS	349 (2)*	–	–
L1346	F	NS	67 (210)	349	415
L1347	F	NS	836 (211)	174	833
L1001	J	NS	886 (120)*	–	2322
L1026	M	NS	1332 (233)	158	1491
L1223	M	NS	467 (195)	343	721
L1226	M	NS	685 (226)	943	596
L1296	M	NS	404 (211)	260	660
L1297	M	NS	110 (211)	244	220
L1005	F	WS	23 (238)	144	139
L1224	F	WS	2103 (132)*	–	–
L1225	F	WS	1049 (57)*	–	–
L1295	F	WS	92 (91)*	–	–
L1299	F	WS	2591 (117)*	–	–
L1349	F	WS	422 (117)*	–	–
L1004	J	WS	483 (239)	60	477
L1006	M	WS	3206 (238)	95	3399
L1023	M	WS	527 (232)	0	527
L1024	M	WS	2118 (233)	0	2118
L1298	M	WS	2893 (211)	2910	5802
L1348	M	WS	1185 (48)*	–	–
L1363	M	WS	5429 (208)	3777	6126
L1367	M	WS	6245 (210)	771	6975
L1368	M	WS	2080 (209)	789	1725

1997 straight-line = point of release to last known 1997 location, 1998 straight-line = 1997 hibernacula to 1998 hibernacula, Final straight-line = point of release 1997 to 1998 hibernacula, F = female, J = juvenile (undetermined sex), M = male, NS = not supplemented, WS = water-supplemented. The numbers of days after release corresponding to each tortoise's last location in 1997 is in parentheses. Asterisks indicate tortoises lost in 1997.

burrows of release. These tortoises ended up 404–6245 m from their initial burrows in 1997. Some tortoises traveled long distances away from the release area in nearly straight-lines and others started traveling in straight-lines, but switched directions after the observation periods on days of release and remained near to the release area. The tendency for some tortoises to travel in straight-lines for long distances after translocation has been described previously (Berry, 1974). In that study, only translocatees that were originally captured in the wild tended to travel far and/or in straight-lines from points of release. Translocatees that were former captives stayed within a few hundred meters of their points of release and did not venture more than 100 m from burrows that they established (Berry, 1974). A recent study of the Gopher Tortoise (*Gopherus polyphemus*), which inhabits the southeastern United States, suggests that fidelity to the release area increases with increased time spent in temporary outdoor enclosures at the site (Tuberville et al., 2005). While there is currently more contiguous habitat remaining for Desert Tortoises than for Gopher Tortoises, there could be situations where reducing movements away from the release area would be desirable and achievable through various methods. Although eliminating water supplementation prior to release did reduce the dispersal of males in our study, it did not appear to affect females similarly.

Homing attempts, especially for short distance translocations, have been shown to be problematic for various species including the Gila Monster (*Heloderma suspectum*), which shares its distribution with the Desert Tortoise (Sullivan et al., 2004). In one study, translocated Desert Tortoises of captive origin showed little to no tendency to orient toward home, while 9 of 12 tortoises of wild origin did orient toward home (Berry, 1974). Eastern Box Turtles (*Terrapene c. carolina*) moved 32–131 km did show a weak, yet variable tendency to home (Cook, 2004). The tortoises in our study did not tend to travel toward home, possibly due to the distance between the LSTS site and their former homes.

4.5. *Mortality*

One might expect that traveling long distances in unfamiliar surroundings would increase translocated tortoises' chances of mortality. Desert Tortoises have good spatial memories and will reuse shelter sites and other resources in locations that are familiar to them (Berry, 1974; Marlow and Tollestrup, 1982). Although the WS males traveled long distances from the release area before reducing their movements, only one WS male died.

The mortality rates of females and males were not significantly different for the LSTS tortoises, however, given the small sample sizes and extremely low male mortality as

Table 3 – Numbers of translocated tortoises lost at the LSTS site

Sex	Experimental group	Total released	Partial carcasses	Intact carcasses	Lost radio signals, no carcass
F	NS	7	1	1	1
F	WS	6	2	1	2
M	NS	5	0	0	0
M	WS	8	0	1	0
J	NS	1	0	0	0
J	WS	1	0	0	0

Partial carcasses had evidence of predation or scavenging. F = female, M = male, J = juvenile (undetermined sex), NS = not supplemented prior to release, WS = water-supplemented prior to release.

compared to females, this question should be addressed with a larger sample size. In a previous study in which translocated and resident tortoises were monitored in plots of irrigated and unirrigated desert habitat, female translocated tortoises were reported to have a higher mortality rate than resident females, resident males, or translocated males (SAIC, 1993). We recalculated mortality rates for tortoises in unirrigated plots from the first two seasons after release by requiring recovery of a carcass for a tortoise to be considered dead. This new analysis of the data indicates that the translocated females had a mortality rate of 20.0% in two activity seasons, while resident females, resident males, and translocated males experienced no mortality (SAIC, 1993).

In times such as drought when predators (e.g. coyotes, kit foxes, bobcats) have fewer mammalian prey available, they will increase take of less preferred prey including tortoises (Woodbury and Hardy, 1948; Berry, 1974). During droughts, coyotes apparently killed most of the tortoises in one study at the DTNA (Peterson, 1994) and 21–28% of the marked wild population in a study near Ridgecrest, California were killed by canids. Predation was the suspected cause of death of most wild resident and first-season translocated tortoises in a study concurrent with ours that took place approximately 30 km to the north at Bird Spring Valley (BSV), Nevada (Nussear, 2004). Although half of the carcasses in our study showed signs of having been eaten, it should not be assumed that predation was the cause of death in all cases (Table 3). It is possible that the tortoises died of other causes and were quickly scavenged, or tortoises may have become dehabilitated and therefore susceptible to predation. Many times the cause of death of released animals is reported to be predation without dehabilitation considered as the ultimate cause (Soderquist, 1994). Two of the three animals whose carcasses were eaten had damp nares, a possible sign of disease, before death.

Wild tortoises were not equipped with telemetry radios at the LSTS site, so a proper experimental control with which to compare the mortality rate of translocatees did not exist. Tortoises translocated to BSV in the spring of 1997 had a total mortality rate of 11.7% (7 of 60 released) that year, while residents at BSV had a mortality rate of 15.1% (8 of 53) that same year (Nussear, 2004). The mortality rates of translocated and resident animals at BSV were not significantly different (chi square = 2.563E−4, df = 1, Fisher's Exact $p > 0.9999$). The mortality rate of 21.4% (6 of 28 released) at the LSTS site was not different from the 11.7% calculated for tortoises translocated to BSV (chi square = 1.445, df = 1, Fisher's Exact $p = 0.3327$). The data from BSV and previous studies suggest that all tortoises at the LSTS site, regardless of translocated or resident status, likely were negatively impacted by drought conditions at the site in 1997. Additionally, a cohort of tortoises that we released at the LSTS site for another experiment in the spring of 1998 had a 2.5% (1 of 40) mortality rate that year, further suggesting that the translocation itself did not strongly influence mortality rates, while drought did.

4.6. *Conservation implications*

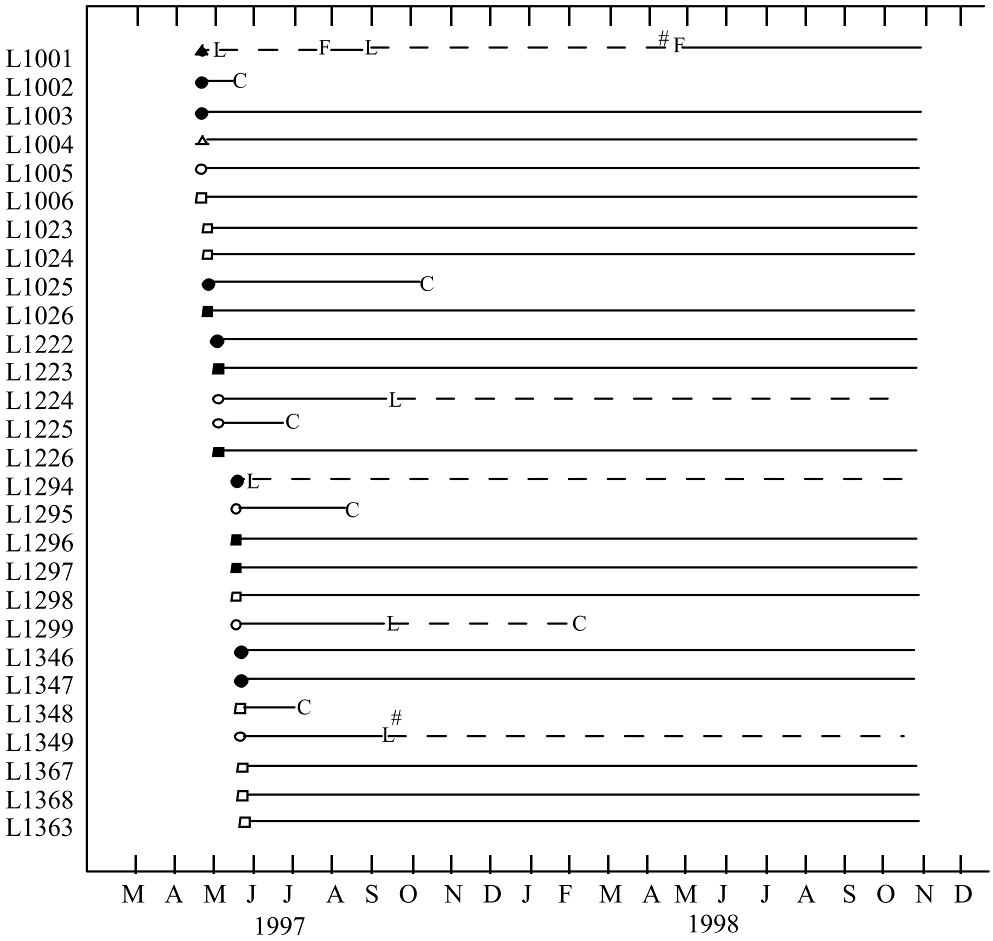
The translocation of tortoises to the LSTS site in spring of 1997 occurred at the end of a period with little rainfall. Annual vegetation was sparse and dry, and there was no rainwater for tortoises to drink until late July 1997. Because the conditions at the LSTS site were harsh, the ability of tortoises to adjust to life in the wild could be examined under adverse conditions. Despite harsh conditions, most of our translocated tortoises quickly became adept at life in the wild. Although initial mortality rates may be lower when translocations occur in years with plentiful rainfall, translocations during dry years may be acceptable because drought conditions likely affect mortality of resident and translocated tortoises similarly. It may be beneficial, however, to release tortoises with unknown histories (e.g. unknown access to sufficient food and water in years prior to translocation) in non-drought years. At small translocation sites or when goals include increased density in particular portions of the site, travel by male tortoises may be reduced by not providing supplemental water from the end of last captive hibernation up to release in spring. We conclude that, regardless of water supplementation regimen, initial success in our translocation demonstrates high potential for longer-term successes. We strongly suggest that translocation be considered a valid tool available for conservation of the Desert Tortoise. Although translocated tortoises fared well during their initial adjustment period, long-term survival and productivity of these animals will be subject to the same factors that continue to dwindle populations of the Desert Tortoise across its range. If we are able to effectively abate the myriad of threats that lessen the likelihood of this species' persistence, translocation of tortoises to appropriate areas will be essential to bolster decimated populations toward a sustainable existence.

Acknowledgements

We thank the US Fish and Wildlife Service; Clark County, Nevada through their Multiple Species Habitat Conservation Plan; and the Biological Resources Research Center at the University of Nevada-Reno for funding our project. Our project site was managed by the Bureau of Land Management, and we thank S. Slone for helping to make this site available. Thanks to J. Bresson, R. Bubb, C. Bulloch, J. Bulloch, M. Damon, N. Dewar, J. Duncan, S. Frantzeskos, R. Goldman, A. Hanlon, A. Hawkins, C. Holmes, K. Johnston, D. Jones, K. Kettenring, A. Knoshaug, A. Mahar, K. Paxson, J. Ranson, P. Sharky, B. Shepard, J. Sikich, M. Taggart, M. Thomas, and E. Vining who assisted in the project as Student Conservation Association Volunteers. B. Tomica, K. Murphy, R. Loubeau, and H. Leach of the US Geological Survey's Biological Resources Division contributed to field work. C. LaBar, M. Berkowitz, and the crew of Southern Nevada Environmental Inc. helped with experimental setup at the Desert Tortoise Conservation Center. S. Jenkins, W. Sweigert and W. Wallace had suggestions on statistical analyses. R. Espinoza, T. Esque, C. Fowler, J. Hayes, K. Nussear, M. Saethre, E. Simandle, and D. Wilson provided comments on drafts of the master's thesis upon which this manuscript is based. We thank Julie Yee and three anonymous reviewers for comments that improved this manuscript. Experiments were conducted according to IACUC guidelines (University of Nevada IACUC Protocols A95/96-19, A98/99-19, A98/99-29, and A95/96-28) and under permits issued by the US Fish and Wildlife Service (PRT-801045 and PRT-702631 with subpermits NBSNER-3 and BRDNER-4) and Nevada Division of Wildlife (S-14528 and S-17841).

Appendix

Release histories of 28 *G. agassizii* at the LSTS site. Release dates are indicated by open shapes for the WS tortoises and by filled shapes for the NS tortoises, with circles for females, squares for males, and triangles for juveniles (unknown sex). L = lost radio signal; C = carcass found; F = live tortoise found; # = known transmitter failure. Solid lines indicate that a tortoise was monitored continuously and dashed lines indicate that a tortoise was lost.



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Effects of Climate Change on Population Persistence of Desert-Dwelling Mountain Sheep in California

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Abstract: *Metapopulations may be very sensitive to global climate change, particularly if temperature and precipitation change rapidly. We present an analysis of the role of climate and other factors in determining metapopulation structure based on presence and absence data. We compared existing and historical population distributions of desert bighorn sheep (*Ovis canadensis*) to determine whether regional climate patterns were correlated with local extinction. To examine all mountain ranges known to hold or to have held desert bighorn populations in California and score for variables describing climate, metapopulation dynamics, human impacts, and other environmental factors, we used a geographic information system (GIS) and paper maps. We used logistic regression and hierarchical partitioning to assess the relationship among these variables and the current status of each population (extinct or extant). Parameters related to climate—elevation, precipitation, and presence of dependable springs—were strongly correlated with population persistence in the twentieth century. Populations inhabiting lower, drier mountain ranges were more likely to go extinct. The presence of domestic sheep grazing allotments was negatively correlated with population persistence. We used conditional extinction probabilities generated by the logistic-regression model to rank native, naturally recolonized, and reintroduced populations by vulnerability to extinction under several climate-change scenarios. Thus risk of extinction in metapopulations can be evaluated for global-climate-change scenarios even when few demographic data are available.*

Key Words: climate change, extinction, hierarchical partitioning, metapopulation, *Ovis canadensis*

Efectos del Cambio Climático sobre la Persistencia de la Población de Borrego Cimarrón en California

Resumen: *Las metapoblaciones pueden ser muy sensibles al cambio climático global, especialmente si la temperatura y precipitación cambian rápidamente. Presentamos un análisis del papel del clima y otros factores en la determinación de la estructura de la metapoblación con base en la presencia y ausencia de datos. Comparamos las distribución actual e histórica de la población de borrego cimarrón del desierto (*Ovis canadensis*) para probar si los patrones climáticos regionales estaban correlacionados con la extinción local. Utilizamos un Sistema de Información Geográfica (SIG) y mapas para examinar todas las cordilleras que tienen o tuvieron poblaciones de borregos en California y calificar variables que describen el clima, la dinámica metapoblacional, los impactos humanos y otros factores ambientales. Utilizamos regresión logística y partición jerárquica para evaluar la relación entre estas variables y el estado actual de cada población (extinta o existente). Los parámetros relacionados con el clima (elevación, precipitación y presencia de manantiales confiables) estuvieron poderosamente correlacionados con la persistencia de la población en el siglo veinte. Las poblaciones en cordilleras bajas y más secas tuvieron mayor probabilidad de extinción. El pastoreo de borregos*

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Paper submitted January 17, 2002; revised manuscript accepted April 18, 2003.

domésticos se correlacionó negativamente con la persistencia de la población. Utilizamos las probabilidades de extinción condicionales generadas por el modelo de regresión logística para clasificar a las poblaciones nativas, recolonizadas naturalmente y reintroducidas por su vulnerabilidad a la extinción bajo varios escenarios de cambio climático. Así, el riesgo de extinción en metapoblaciones puede ser evaluado para varios escenarios de cambio climático aun cuando sólo se disponga de pocos datos demográficos.

Palabras Clave: cambio climático, extinción, metapoblacione, *Ovis canadensis,*partición jerárquica

Introduction

Current climate-change scenarios predict an increase in global air temperature of 1.1–3.3° C over the next century (Houghton 1996; Field et al. 1999). Warmer temperatures during the last 30 years have affected the function and composition of ecological communities and the phenology and distribution of many species (Walther et al. 2002). Population declines and local and global species extinctions have also been linked to this warming trend (McCarty 2001).

As climate warms, vegetation communities shift in composition or distribution. High-elevation plant communities decrease in area, fragment, or vanish (Peters & Darling 1985). Species with fragmented distributions and low dispersal capability may be particularly vulnerable because dispersal to new sites may be limited (Walther et al. 2002). Therefore, species distributed in metapopulations (Levins 1969, 1970) may be at high risk. Climate change that decreases habitat quality or area may increase local extinctions and decrease the number of available habitat patches, conditions that can lead to extirpation of a metapopulation before all habitat becomes unsuitable (Hanski 1999). Moreover, environmental stochasticity or environmental change is usually regionally correlated, which reduces metapopulation size and persistence time (Levins 1969; Hanski 1999). We present an analysis of populations of desert mountain sheep (*Ovis canadensis nelsoni*, as defined by Wehausen & Ramey 1993, 2000) that demonstrates a simple and general way to analyze metapopulation response to climate-related environmental variation using relatively sparse data.

Desert mountain sheep, hereafter referred to as desert bighorn sheep, are desert-adapted ungulates with small population sizes, low dispersal rates (Geist 1971), and naturally fragmented distributions often characterized as metapopulations (Schwartz et al. 1986; Bleich et al. 1990; Bleich et al. 1996). Desert bighorn sheep inhabit numerous, but often small and isolated, desert mountain ranges throughout the Sonoran, Mojave, and Great Basin deserts of the southwestern United States. A few populations are also found in the more mesic Transverse and Peninsular mountain ranges of southwestern California. Most populations of desert bighorn sheep are small, with 41 of 56 extant populations in the state of California estimated at fewer than 100 individuals in 1993 (Torres et al. 1994).

Desert sheep are well adapted to xeric conditions (Hansen 1982), persisting as the climate of the southwestern United States has become increasingly arid since the end of the Wisconsonian glacial period (Van Devender & Spaulding 1979; Spaulding 1990). However, recent regional trends in warming and drying have been particularly severe. From 1901 to 1987, mean annual temperature in the deserts of the southwestern United States increased 0.12° C per decade (Lane et al. 1994). Annual precipitation decreased by roughly 20% over the last century in southeastern California, one of the largest such decreases in the United States (Ball et al. 1998). Because drought can cause increased mortality among desert bighorn sheep (Monson 1960), affect recruitment dynamics (Wehausen et al. 1987), and has perhaps led to population extinction in several cases (Weaver & Mensch 1971), the distribution of desert bighorn sheep may already have been affected by these climatic trends.

Biologists have attempted to estimate the presence and size of bighorn sheep populations within California since 1940, and in some cases earlier records exist (Torres et al. 1994; Wehausen 1999). Although imperfect, this data set presented an opportunity to examine the role of spatial and temporal climatic variation and other factors in the population persistence of desert bighorn sheep. Historic and current population sizes have been estimated variously from ground, waterhole, and helicopter surveys (Torres et al. 1994). The nature and quality of these inventories have varied, but partial population inventories were compiled in 1940, 1946–1948, 1957, 1970–1974, 1979–1985, 1994, and 2002 (Wehausen 1999). Significant population turnover was observed: about 30 of 80 populations of desert bighorn sheep have gone extinct in California during the last 60 years, with an estimated 4300 desert bighorn sheep remaining by 1993 (Torres et al. 1994). Desert bighorn sheep have been reestablished in seven mountain ranges by translocation (Torres et al. 1994) (Fig. 1). Three apparent natural recolonizations have been observed in recent years. It is possible that additional extinctions and subsequent recolonizations were undetected between survey periods.

Additional Causes of Population Extinction

Factors other than climate must be considered in any systematic analysis of turnover of bighorn sheep populations.

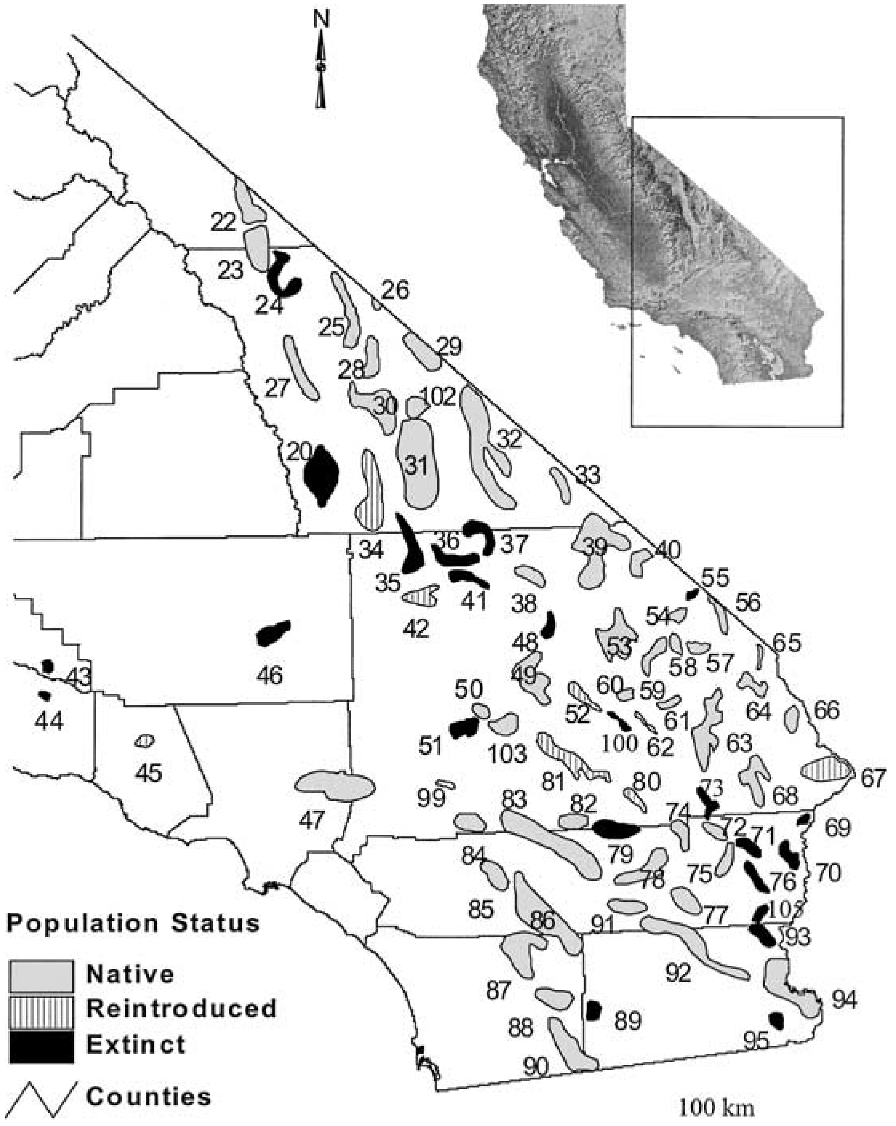

*Figure 1. Native, relocated, and extinct populations of desert bighorn sheep (*Ovis canadensis nelsoni*) in California (from Torres et al. 1994). Numbers are those assigned to the ranges of the populations demarcated by the polygons.*

Many of these factors are related to patterns of historical and current human use. Contact with livestock is detrimental to bighorn sheep because of competition for forage (Hansen 1982) and disease transmission, particularly from domestic sheep (Foreyt & Jessup 1982; Jessup 1985). Feral burros may contribute to the decline of bighorn populations by destroying water holes and competing for forage (Buechner 1960; Hanley & Brady 1977; Dunn & Douglas 1982), but there has been little quantification of subsequent reductions in bighorn numbers (Welles 1962; Jones 1980). Poaching and unregulated hunting have historically reduced populations (Buechner 1960), particularly in areas where mining occurred (Graham 1980), but poaching probably has had little impact in recent times (Weaver 1982). Nonetheless, development and general use of bighorn habitat by humans remains a concern in specific areas (Papouchis et al. 2001; Rubin et al. 2002).

Small population size has been considered an important but controversial predictor of population vulnerability of desert bighorn sheep, although the reasons for variation in population sizes have not been considered (Berger 1990; Krausman et al. 1993, 1996; Goodson 1994; Wehausen 1999). There is little argument, however, that population size is a potentially important factor in population persistence (Caughley 1994). Both Berger (1990) and Wehausen (1999) concurred that small populations of these unique ungulates were more vulnerable to extinction than large ones.

Hypotheses

We predicted that the probability of population extinction of desert bighorn sheep in California would be inversely correlated with climatic factors (temperature and precipitation) that increase annual nutrient availability and with the presence of predictable surface water, which helps desert bighorns survive periods of severe drought. Elevation was used as a surrogate for temperature because of the lack of detailed spatial data on temperature, although it is also correlated with precipitation. Furthermore, elevation can be easily measured in other systems where detailed spatial information on climate is not available. Although numerous human-made water sources have been made available to desert bighorn in California (Bleich & Pauli 1990), we limited analyses to natural water sources as a better reflection of water availability during most of the twentieth century.

We evaluated several other hypotheses concerning the distribution of desert bighorn sheep in California. In most metapopulation patch models, extinction probability decreases with increasing patch area (Hanski 1991, 1997). Extinction probability also decreases with increasing immigration, which, in turn, depends largely on interpatch distance (Levins 1969, 1970; Hanski 1991, 1997). Therefore, we tested the following hypotheses: (1) extinct populations inhabit ranges with smaller two-dimensional area than ranges with extant populations, and (2) extinct populations are more isolated from other mountain ranges containing bighorn habitat than are extant populations.

We evaluated additional plausible influences on desert bighorn sheep persistence to control for possible correlation with climate-related variables. These included geological variation, presence of domestic and feral livestock, and measures of human use of bighorn habitat. Finally, after exploring how regional climatic variation affected population extinction, we used the global-climate-change scenario described by Field et al. (1999) to simulate how the risk of extinction for remaining populations might change over the next century.

Methods

Spatial Analysis of Population Extinction

We scored 80 mountain ranges with extinct or extant populations of desert bighorn sheep in California for average annual precipitation, elevation, isolation, area, presence of dependable natural springs, geologic parent material, domestic sheep and cattle allotments, presence of feral horses and burros, deposits of precious metals, cities and towns, and vehicle access (Table 1). We converted all data from the geographic information system (GIS) to raster format in Universal Transverse Mercator (UTM) projection units and overlaid them on the population map (Torres et al. 1994). Data not based on the GIS were recorded only as presence or absence.

To determine which ranges to include, we updated a GIS map of desert bighorn sheep populations (Fig. 1) compiled by Torres et al. (1994) with population lists from Wehausen (1999). The rough population polygons (Torres et al. 1994) generally were based on the basal contours of each range and were usually defined as areas of contiguous mountainous terrain, separated from other populations by areas of flat desert or low relief. Because dispersal between mountain ranges is extremely limited (Ramey 1995), these populations function largely as independent demographic units. The Mule Mountains (Fig. 1, no. 105) were added to the list based on evidence of beds and fairly heavily used trails (R. Weaver, personal communication).

Elevation and precipitation scores were the map-grid cells with the highest value overlapping each population polygon. Bighorn sheep move easily within mountain ranges and thus can select the best conditions within the area; hence, the highest precipitation and elevation values probably best reflect the range of habitat available for use. We determined the presence of dependable springs by interviewing experts on desert water in bighorn sheep habitat in California (Table 1) and consulting reports on wildlife-accessible desert water sources (Weaver et al. 1968, 1969, 1972; Weaver & Mensch 1970*a*, 1970*b*, 1970*c*, 1971; Weaver & Hall 1971*a*, 1971*b*, 1972, Weaver 1972). For each mountain range, we compiled a list of springs that do not dry up even during extended drought.

We estimated isolation for each mountain range by taking the harmonic mean of the distance from the edge of each population polygon to the edge of the nearest three population polygons (Harrison & Ray 2002) (Table 1). Area was calculated directly from the GIS population polygons.

We scored geologic parent material because the geology of bighorn habitat in the Mojave and Sonoran deserts of California is diverse, and the type and quality of vegetation is often influenced by parent material (Barbour et al. 1980). Resulting variation in forage could affect the persistence of bighorn sheep populations. We examined the percent area of volcanic or granite parent material and the presence or absence of limestone in each range.

We used information from the California Desert Conservation Area (CDCA) plan (Bureau of Land Management 1980) to test whether population extinctions were more common when cattle or domestic sheep grazing allotments, feral burros and horses, and mineral deposits suitable for mining were present in bighorn sheep ranges since population inventories began around 1940. The presence of mineral deposits suitable for mining was the best available index of mining activity, thought to conflict with bighorn sheep as a result of poaching by miners in the earlier periods and habitat destruction (Buechner 1960). We interviewed range and wildlife biologists for the U.S. Forest Service, Bureau of Land Management, Deep Canyon Reserve, and San Diego Zoo (S. Loe, B. Brown, M. Frael, A. Muth, & E. Rubin, personal communications) to score mountain ranges not described in the CDCA plan (Fig. 1, nos. 43, 44, 45, 47, 84, 85, 86, 87, 88, 89, 90, 99). We also determined whether degree of road access and

Table 1. Parameters included in logistic-regression analyses of extinction of desert bighorn sheep populations[a] in California.

Parameter	*Descriptive statistic*	*Data type/description[b]*	*Source[b]*
Precipitation	maximum value in each population polygon	GIS/isohyets of average annual precipitation 1900–1960, 400+ ha resolution	UCLA/Teale Data Center[c]
Elevation	maximum	GIS/3-arc-second digital elevation models, 90 m resolution	UCLA/Teale Data Center
Dependable springs	presence/absence	interviews/experts on wildlife water sources in California	G. Sudmeier (SCBS); R. Weaver (CDFG, retired)
Granite	area (%)	GIS/"Geologic Map of the United States"	King & Beikman 1974
Volcanic rock	area (%)	GIS/"Geologic Map of the United States"	King & Beikman 1974
Limestone	presence or absence	paper/1:250,000 scale geologic maps of California	Jenkins 1958
Isolation	harmonic mean of distance to nearest 3 populations	GIS/"Status of Bighorn Sheep in California, 1994"	Torres et al. 1994
Area	polygon area	GIS/"Status of Bighorn Sheep in California, 1994"	Torres et al. 1994
Distance to towns/cities	minimum distance from sheep polygons	GIS/urban areas (1990 census)	UCLA/Teale Data Center
Mining	presence or absence of "economically viable mineral deposits"	paper/map 11, "Economic Mineral Resources"	BLM 1980
Road access (ordinal)	closed (1), approved roads (2), existing roads (3)	paper/map 10, "Motorized-Vehicle Access"	BLM 1980
Feral burros and horses	presence or absence	paper/map 8, "Wild Horse and Burro Management Area"	BLM 1980
Cattle	presence or absence of grazing allotments	paper/map 9, "Livestock Grazing Allotments"	BLM 1980
Domestic sheep	presence or absence of grazing allotments	paper/map 9, "Livestock Grazing Allotments"	BLM 1980

[a] *Population polygons were drawn by Torres et al. (1994) using the basal contour of each mountain range inhabited or formerly inhabited by desert bighorn sheep.*

[b] *Abbreviations: BLM, Bureau of Land Management; CDFG, California Department of Fish and Game; GIS, geographic information system; SCBS, Society for Conservation of Bighorn Sheep; UCLA, University of California, Los Angeles (mirror site of Teale Data Center, Web site: http://gisdb.cluster.ucla.edu:3080/)*

[c] *Stephen P. Teale Data Center, Web site: http://www.gis.ca.gov/*

minimum distance to towns and cities correlated with extinction (Table 1). We assumed that these measures provided an index of general human activity and that current vehicle access (closed or restricted to varying degrees) reflects historical patterns of use.

Logistic Regression and Model Selection

We combined all parameters in logistic-regression models using an approach similar to that of Sjögren-Gulve and Ray (1996). The response parameter categories were "extinct" or "native" population status. We treated all reestablished populations as extinct because reintroductions (translocations through direct human intervention) and natural recolonizations (Fig. 1, nos. 24, 73, 100) took place in ranges where population extinctions occurred previously. We calculated log-likelihood and chi-squared values using JMPstart (Sall & Lehman 1996).

We tested the univariate model for each parameter and determined that Pearson correlations between all parameters were <0.7, as recommended by Hosmer and Lemeshow (2000) (Table 2). Initially, we explored biologically relevant interaction terms between the variables but found little support for further testing.

We used $\mathrm{QAIC_c}$, a modified version of Akaike's information criterion (AIC) (Burnham & Anderson 1998), for model selection. This statistic corrects for small sample size relative to the number of estimated parameters and for an overdispersion factor between 1 and 4. Overdispersion was estimated as 3.9 from the likelihood-ratio chi-squared value and degrees of freedom of the global model including all 14 parameters (Burnham & Anderson 1998) and may result from correlated environments among adjacent populations. We grouped parameters by category of hypothesis (climate, geology, metapopulation, domestic or feral livestock, and human use) into models and compared $\mathrm{QAIC_c}$ values with univariate and global models. We then combined parameters with strong effects in additional models.

After identifying a series of competing best models, we used hierarchical partitioning to assess the independent and joint effects of each parameter in a single model with all parameters included in the best models (Chevan & Sutherland 1991). Hierarchical partitioning serves as an additional control for multicollinearity and uses a measure of model fit to separate the independent and joint contributions of each parameter by comparing the fit of all models containing a particular parameter to all corresponding

Table 2. Correlation of parameters in global logistic-regression model of desert bighorn sheep population extinction.

Variable	Elev.	Spr.	Grn.	Volc.	Lim.	Iso.	Area	City	Mine	Road	Bro.	Ctl.	D.Shp.
Precipitation	0.65*	0.33*	0.03	−0.21	0.20	0.34*	0.16	−0.36*	−0.05	−0.12	−0.18	0.23*	0.43*
Elevation (Elev.)	—	0.47*	0.07	−0.22	0.49*	0.06	0.35*	−0.09	0.18	−0.22	0.16	0.39*	0.21
Springs (Spr.)		—	−0.03	0.08	0.04	0.08	0.27*	−0.04	0.09	−0.26*	0.14	0.23*	0.21
Granite (Grn.)			—	−0.28*	0.01	−0.04	0.04	−0.22	−0.02	0.04	−0.24*	0.21	−0.02
Volcanic (Volc.)				—	−0.16	−0.06	−0.12	0.30*	−0.18	0.08	0.10	0.10	−0.08
Limestone (Lim.)					—	−0.07	0.18	0.03	0.29*	0.10	0.19	0.33*	0.03
Isolation (Iso.)						—	−0.05	−0.18	0.15	−0.13	−0.15	−0.09	0.66*
Area							—	−0.32*	0.21	−0.10	0.05	0.03	0.06
City distance (City)								—	0.23*	−0.01	0.30*	0.16	−0.17
Mining (Mine)									—	0.13	0.21	0.09	0.04
Road access (Road)										—	0.08	0.05	−0.08
Burros/horses (Bro.)											—	0.08	−0.08
Cattle (Ctl.)												—	−0.04
Domestic sheep (D.Shp.)													—

*Significant Pearson correlation, $p < 0.05$.

models without that parameter. This allows greater confidence that the action of a parameter is not masked in the model by coaction with other parameters (Chevan & Sutherland 1991; Mac Nally 1996, 2000). We used the likelihood-ratio chi-squared statistic for each model as the measure of fit to be hierarchically partitioned (Chevan & Sutherland 1991; Mac Nally 1996). The likelihood chi-squared statistic compares the log-likelihood of the model to that of the reduced model with predictor variables removed (Sall & Lehman 1996). Larger values indicate a better fit.

We used parameters included in the competing best-fit models to evaluate extinction probabilities for all native, naturally recolonized, and reintroduced populations for the next 60 years: the mean and modal times of earliest population estimates for all desert bighorn sheep populations in California were 63 and 60 years, respectively. Logistic-regression models give the probability of transition between response variables for each observation (Sall & Lehman 1996) and therefore can be used to calculate the conditional extinction probabilities for each population with regard to factors considered in the model (Sjögren-Gulve & Ray 1996). To assess future risk to native and reintroduced populations, we calculated extinction probabilities (E) as

$$E_i = \frac{e^{(a+bx_i+cy_i+dz_i)}}{1+e^{(a+bx_i+cy_i+dz_i)}}, \tag{1}$$

where a is a constant, b, c, and d are the parameter estimates for the ith population, and x, y, and z are the corresponding predictor variables.

Using the Extinction Model to Evaluate Climate-Change Scenarios

We modeled how population extinction of desert bighorn sheep in California may change with decreasing precipitation (Ball et al. 1998) and increasing temperature (Field et al. 1999) over the next 60 years by using observed relationships with climate-related variables in the final best-fit extinction models. We used the same model chosen for hierarchical partitioning. A warming trend in climate results in a given average temperature occurring at a higher elevation, and organisms with minimum elevation requirements will be found at higher elevations (e.g., Grabherr et al. 1994). To simulate this, we regressed average maximum daily temperature on elevation from 21 weather stations throughout the study area against station elevation (over station history, usually from about 1940 to present) to calculate the adiabatic lapse rate, or rate at which temperature changes with elevation. Bighorn sheep are largely diurnal, and average daily maximum temperature better reflects the extreme temperatures encountered in daytime during foraging and watering. Further, elevation was most correlated with maximum temperature.

We converted 100-year estimates for future temperature change (Field et al. 1999) to 60-year estimates by assuming a linear rate of change. Using the adiabatic lapse rate, we translated the minimum and maximum predicted temperature changes into "losses" in elevation. We subtracted these elevation losses from each population's elevation score. To simulate a further decrease in precipitation, as was observed in the twentieth century in the study area (Ball et al. 1998), we decreased each precipitation score by 12% (60% of the observed 20% change). Finally, using the chosen best-fit extinction model, we used the modified precipitation and elevation scores to recalculate extinction risk for each population.

Results

Causes of Extinction

The AIC testing revealed three competing models within two ΔQAIC units of the best model, which contained

Table 3. Logistic-regression models of bighorn sheep population extinction in California, with log-likelihood values, number of parameters (*k*) including model parameters, intercept, and residual variance (Burnham & Anderson 1998:17), and $QAIC_c$ values.[a]

Rank	*Model*	*Log likelihood*	*k*	$QAIC_c$	Δ $QAIC_c$
1	precipitation, elevation, sheep	−29.67	5	25.87	0.00*
2	precipitation, springs, sheep	−30.56	5	26.33	0.46*
3	precipitation, elevation, springs, sheep[b] (climate + sheep)	−28.48	6	27.61	1.74*
4	elevation, springs, sheep	−33.12	5	27.63	1.75*
5	elevation	−46.79	3	30.08	2.46
6	water	−47.71	3	30.55	2.93
7	sheep	−48.11	3	30.75	3.14
8	area	−49.82	3	31.62	4.01
9	cattle	−49.99	3	31.71	4.09
10	limestone	−50.80	3	32.12	4.50
11	mining	−51.14	3	32.29	4.68
12	precipitation	−51.31	3	32.38	4.76
13	isolation	−51.59	3	32.52	4.90
14	volcanic	−52.44	3	32.95	5.33
15	burro	−52.50	3	32.98	5.37
16	granite	−52.79	3	33.13	5.51
17	city distance	−52.79	3	33.13	5.52
18	limestone, sheep	−45.43	4	31.61	5.73
19	road access	−50.27	4	34.06	6.45
20	isolation, area, sheep (metapopulation + sheep)	−42.74	5	32.52	6.64
21	isolation, area (metapopulation processes)	−48.55	4	33.19	7.31
22	burro, cattle, sheep (domestic, feral livestock)	−44.95	5	33.64	7.76
23	precipitation, elevation, springs (climate)	−45.00	5	33.67	7.79
24	city distance, roads, mining, sheep (human use + sheep)	−39.75	7	32.47	9.88
25	granite, volcanic, limestone, sheep (geology + sheep)	−44.98	6	36.00	10.12
26	granite, volcanic, limestone (geology)	−50.52	5	36.47	10.59
27	city distance, road access, mining (human use)	−47.51	6	37.28	11.40
28	global model (all parameters)	−23.39	17	55.75	29.87

[a] *Models are ranked by $\Delta QAIC_c$ values (a modified version of Akaike's information criterion); competing models with $\Delta QAIC_c$ values of <2 are marked with an asterisk.*

[b] *Model used for hierarchical partitioning and climate simulations. Coefficients are 11.497549 ± 0.55382193 (negative if dependable natural springs are present) ± 7.2903257 (positive if domestic sheep grazing is present) − 0.0161136 ∗ precipitation − 0.0015005 ∗ elevation (see Eq. 1 and Results).*

the parameters of maximum average annual precipitation, maximum elevation, and presence of domestic-sheep grazing allotments (Table 3). The three competing models included the presence of dependable springs, the presence of domestic-sheep allotments, and either maximum annual precipitation, maximum elevation, or both (Table 3). Extinction was negatively correlated with precipitation, elevation, and dependable springs but positively correlated with the presence of domestic-sheep grazing allotments. We chose to use model 3 (Table 3) for hierarchical partitioning and climate simulations because it included all the parameters in the three competing models.

Hierarchical Partitioning of Parameters

Hierarchical partitioning of model 3 (Table 3) revealed that all four parameters retained in the four best competing models had reasonably large independent effects (Table 4). The action of elevation was largely independent. The presence of dependable springs had the weakest independent effect on the model and a large, positive joint effect, indicating that its action in the model was due in part to a high correlation with precipitation and elevation (Table 2). The presence of domestic-sheep allotments had a large negative joint effect, as did precipitation (Table 4). A likely interpretation is that the presence of domestic-sheep allotments was strongly correlated with precipitation but acted in opposition to it with regard to extinction (Table 2): domestic sheep are primarily grazed in the wetter ranges that otherwise favor the persistence of bighorn sheep populations.

Modeling Climate Change

Elevation explained 94% of the variation in average maximum daily temperature at 21 weather stations throughout the study area ($p < 0.0001$) but only 58% of the variation in minimum daily temperature ($p < 0.0001$). Using the regression of maximum daily temperature on elevation, maximum daily temperature $= -0.0078 \ast$ (meters elevation) $+ 31.687$, we calculated the adiabatic lapse rate (rate at which temperature changes with elevation) as 7.8° C/1000 m of elevation. A mean global temperature increase of 0.7° C over the next 60 years (60% of a 1.1° C

Table 4. Hierarchical partitioning* of third-ranked extinction model of desert bighorn sheep populations in southeastern California, containing maximum annual precipitation, maximum elevation, presence of dependable natural springs, and presence of domestic sheep allotments.

	Precipitation	*Maximum elevation*	*Dependable springs*	*Domestic sheep*
Parameter alone	3.23	12.28	10.43	9.61
Independent effects	7.92	9.80	6.76	24.42
Total independent effects (%)	16	20	14	50
Joint effects	−4.69	2.48	3.67	−14.81
Total joint effects (%)	18	10	14	58

**Hierarchical partitioning uses likelihood ratio χ^2 statistics from logistic regression models as a measure of model fit, and using all possible combinations of models with any of the above four parameters assesses the independent contribution of each variable to model fit. Negative joint effects indicate that a variable acts in opposition to or "suppresses" other variables. The sum of the independent and joint effects for each parameter equals the χ^2 statistic of the univariate model for that parameter.*

increase over the next century) thus translates to a "loss" of 85 m elevation in our climate-change simulations. An increase of 2.0° C over the next 60 years translates to a loss of 254 m. We assumed no change in the availability of surface water and set all domestic-sheep allotment scores to "zero" because domestic-sheep allotments are generally no longer permitted on desert bighorn habitat (K. Allison, personal communication).

In the minimum temperature-change scenario of +0.7° C in the next 60 years (Field et al. 1999), average extinction probabilities of native populations increased only slightly, from 0.21 to 0.22. However, in the maximum temperature-change scenario of +2.0° C in the next 60 years, average risk of extinction increased substantially to 0.26. Extinction risk also increased drastically when precipitation was reduced, such that a 0.7° C increase combined with a 12% decrease in precipitation elevated extinction probabilities to levels observed with a 2.0° C increase with no change in precipitation. Average extinction risk increased from 0.21 (no change) to 0.30 when a 2.0° C increase was combined with a 12% precipitation decrease.

Discussion

Elements in the Final Model

Extinction of desert bighorn populations in California in the twentieth century did not occur randomly. Populations in mountain ranges of lower elevation were much more likely to become extinct, particularly at <1500 m (Fig. 2a). Populations in regions with the lowest annual precipitation, especially <200 mm annual precipitation, were also more likely to become extinct (Fig. 2b), as were populations without dependable springs and populations in which domestic-sheep grazing allotments formerly overlapped or abutted desert bighorn habitat. This suggests not only that desert bighorn sheep are vulnerable to climate warming but that climate warming has already affected their distribution in California.

Hierarchical partitioning established that elevation and precipitation each had relatively strong independent effects in the model, despite their high degree of colinearity (Table 4). We suggest that the correlation between low elevation and higher risk of extinction resulted largely from the highly predictive relationship between elevation and temperature. Lower mountain ranges experience higher temperatures, and, as a result, bighorn sheep could have a greater dependency on water sources or poorer nutrition, resulting in lower survival. Higher-elevation ranges have an extended growing season: spring growth starts first at the lower elevations, and green-up progresses up the elevation gradient. Therefore, taller

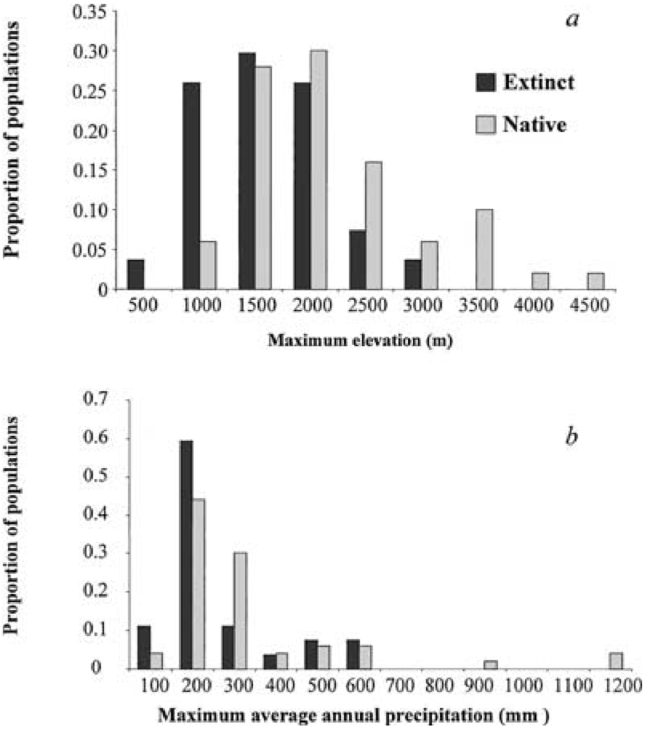

*Figure 2. Distribution of (a) maximum elevation and (b) maximum average precipitation values for ranges of native and extinct bighorn sheep (*Ovis canadensis nelsoni*).*

mountains have some green vegetation and thus better forage for much longer periods than low-elevation ranges (Wehausen 1980, 1992).

The relationship between extinction and precipitation probably results from the dynamics of water availability, soil moisture, and forage quality. Shrub cover in the Mojave Desert strongly correlates with mean annual precipitation (Beatley 1974). In arid regions even a slight decrease in moisture content, whether through increased temperature and increased evapotranspiration or through a decrease in precipitation, could have drastic effects on diet quality and therefore demography. Douglas and Leslie (1986) found that precipitation during gestation accounts for the largest proportion of variability in lamb survival. Wehausen et al. (1987) detected a positive relationship between winter precipitation and recruitment in the Santa Rosa Mountains of California (Fig. 1, no.86). Thus, precipitation apparently plays a large role in reproductive success. More explicit spatial data describing temperature and precipitation may further clarify these relationships.

The absence of dependable natural springs was also correlated with extinction, although this relationship was weaker than that of other model elements (Table 4). Nonetheless, bighorn sheep in many ranges make extensive use of springs and water holes, occur close to water during hot summer months (Andrew et al. 1997, 1999), and physiologically depend on ready access to water during summer (Turner & Weaver 1980).

Extinction of populations of desert bighorn sheep in California was not sensitive to patch size (two-dimensional area of the inhabited mountain ranges). This was surprising because patch size is often considered the most important predictor of population persistence (Hanski 1999; but see Fleishman et al. 2002), and this effect has been detected in Rocky Mountain bighorn sheep (*O. c. canadensis*) (Singer et al. 2001). The strong effect of patch size on persistence is thought to result from the expected correlation with population size if populations are strongly regulated by density dependence. If populations are regulated by environmental factors, however, one can expect a much weaker relationship between patch size and population size (Andrewartha & Birch 1954). Our findings that precipitation and elevation, but not patch size, were correlated with population extinction are consistent with strong environmental regulation of desert bighorn sheep populations.

Population isolation also did not affect extinction in our analysis. We measured isolation as the harmonic mean of the distance to the nearest three mountain ranges used at some time by bighorn sheep, but when adjacent populations were extinct, distances to the nearest inhabited patches may have been much greater. We could not use these distances as a measure because the timing of extinctions are poorly known. However, populations of desert bighorn sheep are generally demographically independent because of low female dispersal rates (Ramey 1995; Boyce et al. 1999). Although extinctions may appear regionally clustered (Fig. 1), this is probably a result of autocorrelated environmental factors such as precipitation.

Higher risk of extinction in lower, drier ranges was detected despite significant correlation of higher precipitation and higher elevation with sheep and cattle grazing and proximity to cities (Table 2). However, elements not retained in final models may still be important to consider during management on a case-by-case basis. Our conditional "extinction probabilities" (Fig. 3) are related solely to variables included in the final best-fit models. Thus, our models provide potentially biased estimates of extinction probabilities that are not all-inclusive.

Evaluating How Climate Change May Influence Population Extinction

Although crude, these climate-change simulations demonstrate that global warming could have serious consequences for desert bighorn sheep, particularly if coupled with decreases in precipitation. Other scenarios can be evaluated with these models as climate projections change. Absolute extinction probabilities should always be viewed with caution (Beissinger & Westphal 1998), but they provide a way to compare the vulnerability of populations to specific threats.

Changes in precipitation patterns, which are more difficult to predict than changes in temperature (Field et al. 1999), could balance or amplify the effects of changes in temperature because precipitation may be more limiting than temperature in these ecosystems (e.g., Wehausen et al. 1987). Careful analyses of how precipitation and temperature affect the growing season of forage plants, and thus diet quality among sheep, may improve future models of the population persistence of wild sheep. Climate warming may have more complicated or more detrimental effects when competition, predation, and disease affect desert bighorn sheep.

Our results have important implications for management actions. For future reintroductions of desert bighorn sheep, managers should consider expected precipitation and elevation within the mountain range of consideration. We do not advocate abandoning all efforts in mountain ranges that are at high risk: some may serve as valuable "stepping stones" for gene flow or demographic "rescue" (Bleich et al. 1990), and the extinction model may not be correct for all locations at all times. However, knowledge of climate-based risk of extinction may allow managers to focus further efforts on locations with the highest probability of success. Understanding which populations are under the most climate-related stress could also be critically important in coming decades (Fig. 3). Because of regionally correlated environmental conditions, whole regions of populations and subsequent opportunities for gene flow or recolonization may be lost (Fig. 3).

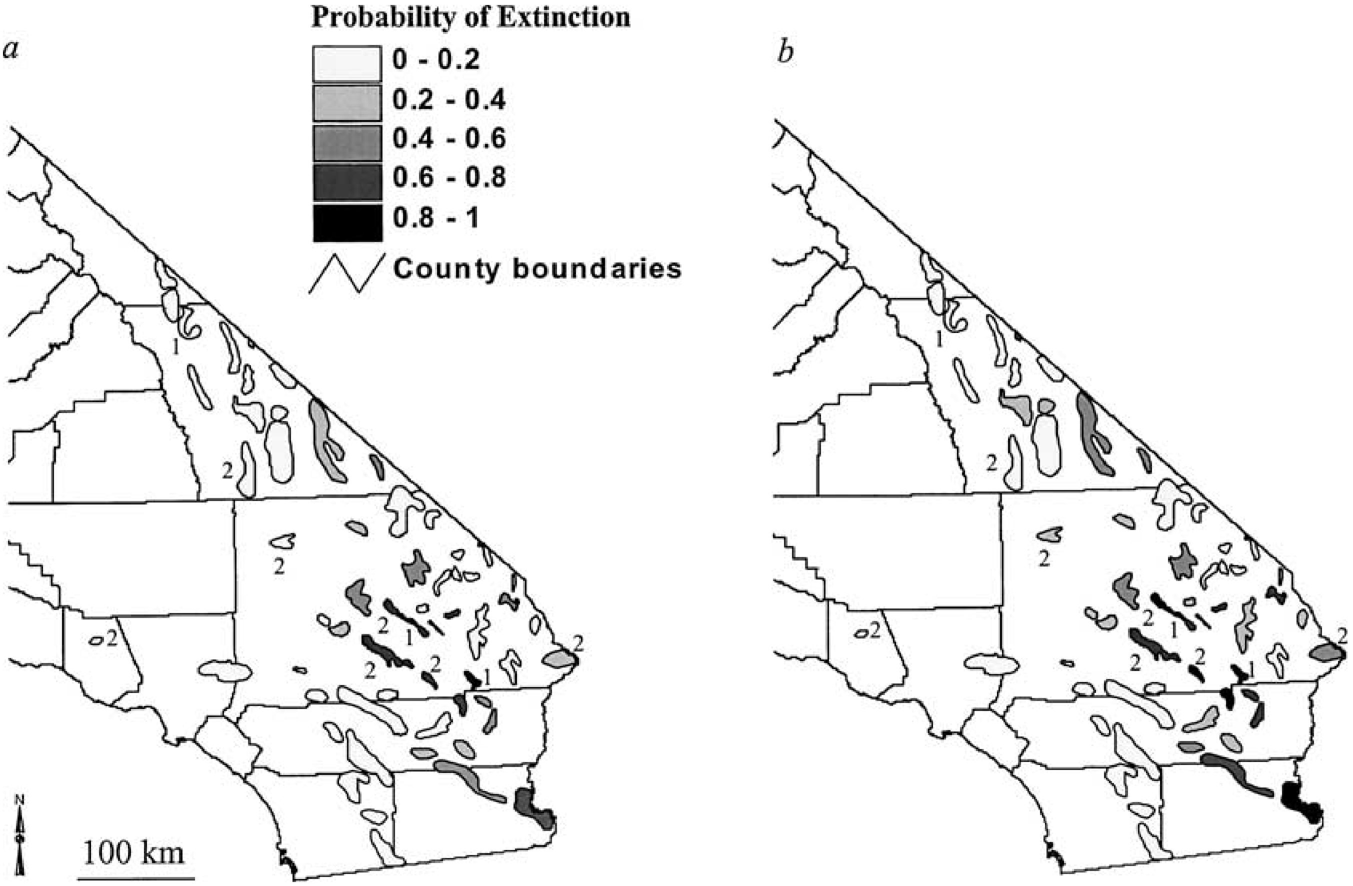

*Figure 3. Conditional extinction probabilities for unnumbered, native desert bighorn sheep (*Ovis canadensis nelsoni*); 1, desert bighorn sheep naturally recolonized since 1994; and 2, reintroduced populations of desert bighorn sheep for the next 60 years; assuming (a) no further climate change and no interactions with domestic sheep or (b) the maximum predicted increase in global temperature (+2.0° C), a 12% decrease in precipitation, no change in surface-water availability, and no interactions with domestic sheep.*

Heightened monitoring of population size, condition, and water availability, with appropriate action, may be necessary to conserve populations of desert bighorn sheep in the future.

The changes in the distribution of desert bighorn sheep observed in the twentieth century are consistent with directional climate change, but we cannot rule out the action of climatic stochasticity. It may be that the distribution of the desert bighorn in California has fluctuated for centuries, with expansion into areas of poorer habitat during cooler and wetter periods and retreat during times of increased drought frequency and intensity. Although the relationships between local climate and extinction are clear, whether current trends are the result of long-term climate change is not.

Using presence and absence data, we demonstrated that population extinctions of desert bighorn sheep in the twentieth century are consistent with a range contraction to areas of higher elevation and greater precipitation. Updated and more detailed climate scenarios can be explored through the relationships with extinction risk, elevation, and precipitation described here. This approach demonstrates that simple population viability analysis can sometimes be conducted even when detailed demographic data are absent. A similar approach might be used in systems where no prior population surveys existed, if suitable criteria for identifying empty habitat patches existed, in a variation of the incidence-function approach used by Hanski (1999) to parameterize metapopulation models.

Many species, particularly those in arid or montane regions, may have already suffered some effects of global climate warming. Elevational shifts in distribution consistent with climate change have been detected in Edith's checkerspot butterfly in the Sierra Nevada of California (Parmesan 1996), montane trees (Fisher 1997), and species in the cloud forests of Costa Rica (Pounds et al. 1999). Sparse data on population size and distribution may have hampered our ability to detect these changes elsewhere. Desert bighorn sheep may serve as a model to help us understand how similar systems may react to the coming changes.

Acknowledgments

We thank R. Weaver and G. Sudmeier for sharing their encyclopedic knowledge of desert waterholes, and S. Loe, B. Brown, M. Frael, A. Muth, E. Rubin, K. Allison, and S. Ostermann for their assistance in determining mining and livestock use on bighorn range. R. Mac Nally and T. Epps provided help with hierarchical partitioning. We would also like to thank S. Beissinger and several anonymous reviewers for thorough and insightful suggestions that greatly improved this paper.

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Ecology Letters, (2005) **8**: 1029–1038 doi: 10.1111/j.1461-0248.2005.00804.x

LETTER

Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep

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Abstract

The rapid expansion of road networks has reduced connectivity among populations of flora and fauna. The resulting isolation is assumed to increase population extinction rates, in part because of the loss of genetic diversity. However, there are few cases where loss of genetic diversity has been linked directly to roads or other barriers. We analysed the effects of such barriers on connectivity and genetic diversity of 27 populations of *Ovis canadensis nelsoni* (desert bighorn sheep). We used partial Mantel tests, multiple linear regression and coalescent simulations to infer changes in gene flow and diversity of nuclear and mitochondrial DNA markers. Our findings link a rapid reduction in genetic diversity (up to 15%) to as few as 40 years of anthropogenic isolation. Interstate highways, canals and developed areas, where present, have apparently eliminated gene flow. These results suggest that anthropogenic barriers constitute a severe threat to the persistence of naturally fragmented populations.

Keywords

Gene flow, genetic diversity, habitat fragmentation, metapopulation, *Ovis canadensis*, road.

Ecology Letters (2005) 8: 1029–1038

INTRODUCTION

As the level of connectivity among human populations continues to increase, natural populations of plants and animals are becoming increasingly isolated. Today the earth's surface is partitioned by an estimated *c.* 28 million km of highways (CIA 2003) that restrict the movement of many species (Trombulak & Frissell 2000; Underhill & Angold 2000). This loss of connectivity is suspected to impede exchange of individuals among populations, thereby accelerating the loss of genetic diversity because of genetic drift (Frankel & Soule 1981; Hedrick 2005). Reduced genetic diversity is likely to increase population extinction rates both in the short term (because of inbreeding, Saccheri *et al.* 1998; Westemeier *et al.* 1998; Coltman *et al.* 1999) and in the long term by reducing evolutionary potential, i.e. the ability of a population to adapt to future changes in biotic and abiotic factors such as climate change (Frankel & Soule 1981; Lande 1998; Fraser & Bernatchez 2001; Hedrick 2005). However, recently constructed barriers have rarely been found to affect genetic diversity in natural populations, particularly for long-lived, large-bodied species (e.g. Kyle & Strobeck 2003; Sumner *et al.* 2004). While roads have been shown to restrict gene flow for species with small body size or relatively low vagility such as amphibians (Reh & Seitz 1990) and beetles (Keller & Largiader 2003), there is growing concern that a much wider variety of taxa may be affected (e.g. Kramer-Schadt *et al.* 2004; Malo *et al.* 2004).

The objective of this study was to assess the effects of major highways and other recently constructed anthropogenic barriers upon genetic diversity in a metapopulation of *Ovis canadensis nelsoni* (desert bighorn sheep). In the desert regions of California, local populations of this long-lived, vagile mammal are often less than 50 individuals (Torres *et al.* 1994). Restricted largely to the steep, rocky mountain ranges that are scattered across the region, these populations are demographically independent and naturally fragmented by the intervening desert (Bleich *et al.* 1990). As resources are variable and local population extinctions common (Epps *et al.* 2004), some connectivity among populations is presumed essential to maintain the regional bighorn sheep metapopulation (Bleich *et al.* 1996). However, the southwest USA has been subject to an increasing degree of urbanization by humans, marked by widespread construction of interstate highways and water canals in this desert region over the last 40–70 years. Anecdotal evidence suggests that bighorn sheep rarely cross these continuously fenced barriers (Bleich *et al.* 1996). Thus it is likely that these barriers on the landscape have reduced connectivity among populations of desert bighorn sheep and possibly many other terrestrial species.

We examined putatively neutral genetic variation across desert bighorn sheep populations in southeastern California (Fig. 1) to assess whether human-made barriers have affected dispersal and genetic diversity to a significant degree. We also defined the geographical scale of current gene flow among these populations and considered the conservation implications of continuing anthropogenic fragmentation.

METHODS

The study area was comprised of the central Mojave, southern Mojave and Sonoran Desert regions of California. Habitat quality for desert bighorn sheep in these arid areas was strongly affected by the spatial and temporal variation in climate and population turnover is high (Epps *et al.* 2004). Apparent dispersal barriers erected in the 20th century include the Colorado River Aqueduct (constructed in the 1930s), urban development, the establishment of large mining operations in Lucerne Valley, the portion of State Highway 62 with four lanes and a concrete median barrier, and interstates 10, 15 and 40 (constructed in the 1960s) (Nystrom 2003). These barriers are largely continuous and have direct physical impediments to locomotion by bighorn sheep, including fences and steep concrete walls. Underground portions of the Colorado River Aqueduct (passing beneath several populations in the southeastern part of the study area) were not considered to be barriers. Major highways were by far the most common barriers between study populations.

We collected genetic samples across the study area during 2000–2003 from 27 populations with varying levels of anthropogenic isolation (Fig. 1). Estimated median population size for these populations was 38 individuals, range was 12–300 (Torres *et al.* 1994). Populations were defined as previously in a geographical information system (GIS) (Torres *et al.* 1994; Epps *et al.* 2004, 2005a), based upon the topographical features of the mountain ranges where they are found. We collected samples from all known populations within the focal study area, except five ranges containing individuals translocated from other populations in the region (Torres *et al.* 1994) (Fig. 1).

We used faecal pellets as the primary source of genetic material, obtained mostly during summer months when desert bighorn sheep congregate at water sources. We collected fresh pellets from observed bighorn sheep or selected the most recent-appearing pellets in the vicinity. Faecal samples were air-dried and stored in paper bags in a dry environment. We also obtained blood and tissue samples from bighorn sheep captured by the California Department of Fish and Game or killed by hunters during 2000–2004. We extracted genomic DNA from faecal samples using a modified DNA Stool Mini-Kit^{TM} (Qiagen, Valencia, CA, USA) protocol (Wehausen *et al.* 2004), and from blood and tissue samples using DNEasy Tissue Kits^{TM}

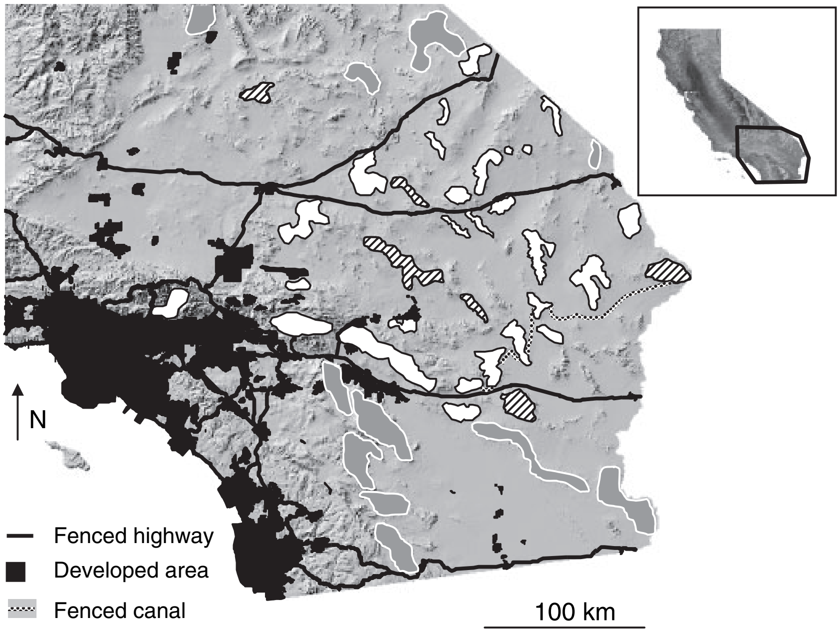

Figure 1 Topographical map of southern California with location and approximate size of the 27 desert bighorn sheep populations sampled (white polygons). Barriers, including canals, interstate highways, freeways, and urban areas, are represented in black or checkered (above-ground portions of the Colorado Aqueduct) patterns. Artificially translocated populations (cross-hatched) and other extant populations where sampling did not occur are also depicted (light grey polygons). Barriers outside the area of sampled populations are not fully represented.

(Qiagen). Before genotyping, we assessed extraction quality by amplifying a *c.* 200-bp fragment of nuclear DNA from the zinc-finger protein gene [Appendix S1(a)]. We visualized the amplification product on 2% agarose gels pre-stained with ethidium bromide; samples generating weak amplifications were not used in further analyses.

We genotyped 14 dinucleotide microsatellite loci for each DNA extraction [Appendix S1(b)]. We conducted a minimum of four replicate polymerase chain reactions (PCRs, Mullis *et al.* 1986) per faecal sample per locus to minimize genotyping errors resulting from degraded DNA (Taberlet *et al.* 1999), and conducted two replicate PCRs for blood and tissue samples. Alleles included in the final consensus genotypes were observed at least twice; if observed only once, an additional four replicates were conducted. We included two negative controls and two positive controls (samples with known genotypes) with every 96 PCR reactions as checks for contamination and to standardize genotypes among experiments.

We estimated the probability of an erroneous genotype because of allelic dropout (selective amplification of only one allele in a heterozygote because of low amounts of template DNA, Taberlet *et al.* 1999). We accomplished this by summing the observed number of allelic dropouts for each locus, and dividing this sum by the number of successful PCR reactions (i.e. the presence of an amplification product) for heterozygous individuals (allelic dropout could only be identified in the case of individuals determined to be heterozygous). Because we had a minimum criterion that each allele per sample per locus had to be observed at least twice (at least two successful replicate PCR reactions with identical results), we squared each per-locus dropout rate to estimate the probability of two dropouts in the same sample. We then summed these squared dropout rates over all loci, and added the average probability of a false allele over 14 loci (calculated from observed rates) to obtain our final estimated probability of a genotypic error per individual. While this method does not account for variability among samples (e.g. Miller *et al.* 2002), we assumed that pre-screening of extractions limited sample variability to a large degree.

We limited further data analyses to samples for which complete genotypes were obtained at all loci. We used the probability of identity (P_{ID}) to identify and eliminate duplicate genotypes resulting from the collection of more than one faecal sample from some individuals. DNA extractions from different faecal samples were inferred as originating from the same individual if the combined P_{ID} for a full-sib relationship was estimated at $< 10^{-2}$ using GIMLET (Valiere 2002), at the number of loci matching between a pair of different DNA extractions (which could be any number of loci less than the maximum of 14 employed in this study). This threshold level of P_{ID} was chosen because most population sizes were estimated at < 100 individuals (Torres *et al.* 1994); 10^{-3} was used for populations > 100. This analysis was undertaken in two steps; first within each population, and then subsequently for all populations combined and treated as a single panmictic population (after removal of all but one of each unique genotype in each population), to detect if any individuals were sampled in more than one population. We assessed the final data set obtained in this manner for any significant deviations from linkage disequilibrium and the expected Hardy–Weinberg genotype frequencies in each population using GENEPOP (Raymond & Rousset 1995).

We also assessed the diversity of mitochondrial DNA haplotypes in each population. Female bighorn sheep are less likely to move between mountain ranges (Festa-Bianchet 1991; Jorgenson *et al.* 1997); therefore maternally transmitted mitochondrial DNA provided an opportunity to assess female dispersal patterns. After identifying unique samples using the microsatellite data, we sequenced 515 nucleotides in the mitochondrial control region from each individual (except three samples that failed to amplify) [primers and protocols are described in Appendix S1(c)]. We sequenced all samples in both forward and reverse directions, editing and aligning them manually, to minimize sequence ambiguities. We used the number of unique haplotypes present in each population as a measure of female-mediated genetic diversity. To correct for variation in sample size, we subsampled each population 100 times using the minimum sample size and calculated the average number of unique haplotypes detected per population.

From the microsatellite data, we estimated the degree of genetic divergence among populations as F_{ST} (and thus Nm) for each population pair using GENEPOP (Raymond & Rousset 1995). F_{ST} rather than R_{ST} (Slatkin 1995) was used because F_{ST} is a more appropriate statistic for 'stepping stone' population models and systems where migration rate exceeds mutation rate (Hardy *et al.* 2003), as is most likely for these desert bighorn sheep populations given numerous observations of colonizations and dispersal between mountain ranges (e.g. Epps *et al.* 2005a,b). Furthermore, F_{ST} performs better when number of loci < 20 (Gaggiotti *et al.* 1999). We used allelic richness (the average number of alleles per locus or A) as our measure of genetic diversity in each population. We used FSTAT (Goudet 1995) to correct A for differences in sample size, as recommended by Leberg (2002). The smallest population sample size was employed as the global sample size.

To determine if human-made barriers (see below) had affected population genetic diversity, we used information theoretic model selection techniques (Burnham & Anderson 1998) to test multiple regression models incorporating either of two estimates of the degree of isolation for each population. We estimated isolation as (i) the harmonic mean of the geographical distance to the nearest three populations (e.g. Harrison & Ray 2002), which weights the mean towards the smallest distance, or (ii) the harmonic mean of the geographical distance to the nearest three populations, but with a 'barrier effect distance' added to the geographical distance between each population pair separated by a human-made barrier. These measures are referred as $\text{isolation}_{\text{distance}}$ and $\text{isolation}_{\text{distance+barriers}}$.

To quantify the above-mentioned barrier effect distance, we estimated the reduction in the relative gene flow parameter (*Nm*) caused by barriers among our study populations. The barrier effect distance was defined as the geographical distance yielding an equivalent decrease in the estimate of *Nm*. We first defined barriers as fenced highways, canals and areas of high-density urban development, and added them to the above employed GIS map. We then employed multiple regressions on all pairwise population comparisons to estimate the degree of correlation between geographical distance and *Nm* among populations that were (i) separated by human-made barriers and (ii) those that were not. Populations were considered as separated by human-made barriers if a straight line between the two closest edges of the population polygons intersected such a barrier. Connecting lines for all pairwise comparisons were generated in the GIS (Jenness 2004) and overlaid on the barrier map to determine which lines intersected barriers. Interpopulation geographical distances were estimated as the shortest distance between the edges of each population polygon (Jenness 2004).

Nm was estimated as $[F_{\text{ST}} = 1/(1 + 4\ Nm)]$ (Wright 1921). The difference between the intercepts of the *y*-axis in the two regressions (denoted as ΔNm) was inferred to result from the effect of human barriers on the degree of genetic isolation (Fig. 2). Finally, we used the coefficient of the regression of population pairs without barriers ($\text{slope}_{\text{no barriers}}$) to estimate the barrier effect distance (in km) as log(barrier effect distance) $= \Delta Nm/\text{slope}_{\text{no barriers}}$.

After defining these two measures of population isolation ($\text{isolation}_{\text{distance}}$ and $\text{isolation}_{\text{distance+barriers}}$), we tested which measure explained the most variance in both *A* and mtDNA haplotype diversity. For both sets of genetic data, we used Akaike's Information Criterion with the small sample size correction (AIC_c) and Akaike weights (Burnham & Anderson 1998) to infer the best regression models. We estimated the overdispersion correction factor ($\hat{c}$) from the deviance of the most saturated model, as described by Lindsey (1999), to ensure that AIC_c rather than the quasi-likelihood information criterion (QAIC_c) was most appropriate. We also tested whether other factors such as population polygon area and estimated current population size (which affects the rate of genetic drift) improved regression models.

We estimated the rate of reduction in genetic diversity (*A*) in those populations affected by human-made barriers by comparing the difference in the predicted level of genetic diversity with the existent barriers (obtained from the regression of *A* on $\text{isolation}_{\text{distance+barriers}}$ described above), and the predicted level of genetic diversity using the same equation but removing the barrier effect for each population. The resulting difference was then extrapolated over the average estimated age of the barriers.

We also analysed pairwise estimates of *Nm* using partial Mantel tests (Smouse *et al.* 1986; Manly 1991) to determine whether relative gene flow was affected by barriers, and at what spatial scale. We repeated this analysis using F_{ST} for comparison, although F_{ST} appeared to be subject to very high overdispersion in other analyses of this data set (not shown). *Nm* represents the amount of gene flow in an idealized Wright–Fisher island model that would yield the observed degree of genetic heterogeneity. Hence, *Nm* cannot be inferred to represent an estimate of the actual

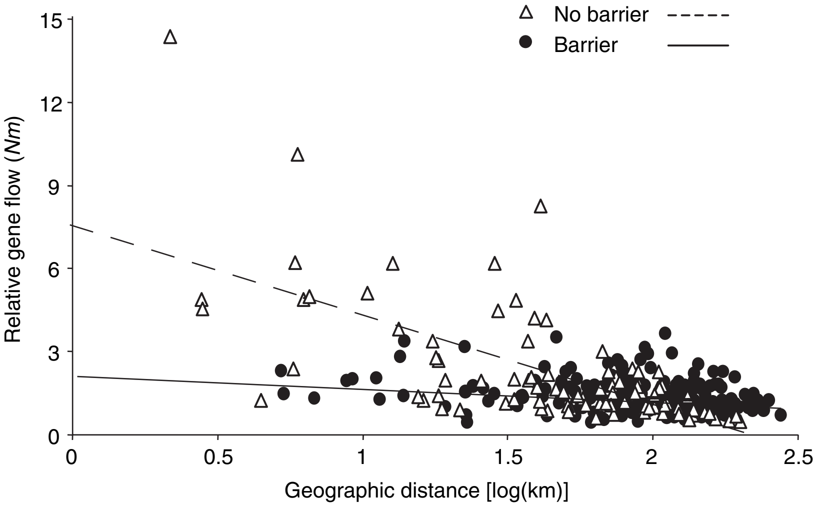

Figure 2 Pairwise population comparisons of migrants per generation (*Nm*, estimated from genetic distance F_{ST}) regressed on log(geographic distance in km). Comparisons are grouped by presence (dark circles) or absence (open triangles) of an intervening barrier. R^2 of pairs without barriers = 0.43, R^2 of pairs with barriers = 0.08. Regression lines are extended to cross the *y*-axis; difference in intercepts was used to calculate the 'barrier effect' (see text).

number of migrants (Whitlock & McCauley 1999). Under such a model *Nm* is correlated to F_{ST}, but in a nonlinear manner and thus we have used both metrics in our estimation. While our population is likely not in mutation-drift-migration equilibrium, *Nm* (and F_{ST}) can provide insights as to the relative levels of gene flow, especially when the rate of gene flow is larger than mutation (Slatkin 1993).

We employed partial Mantel tests over sequential geographical distance classes (0–15, 15–30, 30–60, 60–90, 90–120, 120–150 and > 150 km) (Legendre & Fortin 1989; Bjornstad *et al.* 1995; Dodd *et al.* 2002) to assess the partial correlation of barriers and geographical distance with *Nm* for each distance category. This allowed us to infer the spatial scale at which recent gene flow has occurred or has been disrupted by barriers. For a given distance category, interpopulation distances falling within that range were denoted as '1', all others as '0'. Similarly barriers were noted as '1' (present) or '0' (absent) for population comparisons within the given distance category. In this assessment, we excluded the Coxcomb Mountain population. Most of the bighorn in the Coxcomb Mountains were found to have immigrated from a nearby population, which was established by translocation from a distant population (Epps *et al.* 2005b). While the validity of estimates of type I error (here, falsely concluding that correlation of one independent matrix with the dependent matrix exists, because of correlation with a second independent matrix) in partial Mantel tests has been questioned (Raufaste & Rousset 2001; Rousset 2002), Castellano & Balletto (2002) argued that under even high levels of correlation between the independent matrices, partial Mantel tests closely approximate true type I error.

Finally, we employed the computer program SIMCOAL (Excoffier *et al.* 2000) to investigate if barriers could create a detectable increase in genetic distance between populations, given the time scale and data richness that apply to this study. Coalescent simulations were conducted under two different models, each simulating two adjacent populations 5 km apart. In the first model, we tested the effects of a recently constructed barrier by simulating two populations at mutation-drift-migration equilibrium except during the last seven generations (*c.* 42 years; Coltman *et al.* 2003), when *Nm* was set to zero. No such reduction in *Nm* was added to the second model. In each model 40 gene copies were sampled at each of 14 loci. SIMCOAL uses a pure stepwise migration model (in this case, without constraint on allele size), and requires the user to set migration rate *m*, effective population size *N* and mutation rate μ. SIMCOAL immediately multiplies these parameters to obtain *Nm* and θ, where $\theta = 4N\mu$. To obtain realistic values of *Nm* and θ for use in the model, we estimated $Nm = 6.2$ from the observed estimate of $F_{ST} = 0.039$ between a representative pair of mountain ranges, the Marble and South Bristol Mountains, that are separated by only 5 km with no intervening barrier. We estimated θ from the variance in allele size as $\theta = 2 \times$ (variance in allele size) (Wehrhahn 1975) for both of these mountain ranges ($\theta = 9.62$ and 8.32 respectively), and used the average of these values ($\theta = 8.97$) in our simulation. We also estimated θ from expected heterozygosity as $H_e = 1 - (1 + 2\theta)^{-1/2}$, giving an average of $\theta = 3.27$. For comparative purposes, we tested both of these measures of θ in our simulations, as well as $\theta = 1$. We varied values of *Nm* to include 2, 6.2 and 10. We calculated population pairwise F_{ST} between the two simulated populations for each simulation run using Arlequin (Schneider *et al.* 2000). For each parameter set, 1000 simulation runs from both models were compared to determine the average increase in F_{ST} because of barriers.

We compared this simulated average increase in F_{ST} because of barriers (for populations 5 km apart) to the observed increase in F_{ST} resulting from barriers for populations separated by this distance. We estimated the observed increase by regressing F_{ST} on log(geographic distance) for all population pairs with intervening barriers and for all population pairs without intervening barriers, and calculated the difference in the predicted F_{ST} values at 5 km using these two regression equations.

RESULTS

We obtained complete genotypes at all 14 microsatellite loci from 461 faecal and 47 blood or tissue samples. From our analyses of these 508 genotypes, we inferred that they represented a total of 397 individuals, yielding a mean sample size per population of 15 individuals (range 6–29, SD 5.9; Appendix S2). We identified 21 unique mtDNA haplotypes from 394 of these individuals; one haplotype had been previously described (GenBank no. AF076912, Boyce *et al.* 1999). New haplotype sequences were submitted to the GenBank database under the accession numbers AY903993–AY904012. Numbers of alleles and haplotypes per population, *A*, expected heterozygosity and other basic data are described in Appendix S2.

In the final microsatellite data set, we did not observe any case of allelic dropout among the consensus genotypes of the 111 samples that we identified as duplicates of previously sampled individuals. We found no evidence of linkage disequilibrium within populations after correcting for multiple comparisons.

The average rate of allelic dropout per locus per replicate for the faecal samples was estimated at 3.7%, while rate of occurrence of false alleles was estimated at 0.062%. Overall this yielded a final estimate of 0.022 genotypic errors per individual. Given an error rate of 0.022, in a sample set of *c.* 400 individuals typed at 14 loci, the expectation is approximately 10 single-locus errors in consensus genotypes.

Because this estimated error rate assumes that every sample is heterozygous at all loci, and that there were only two replicate PCR amplifications at each locus, this estimate of the genotype error rate is likely higher than the actual rate: most samples were successfully amplified three to four times. Assuming that genotype errors were randomly distributed with respect to population, this error rate was unlikely to bias our estimates of genetic diversity and divergence in a significant manner for the purposes of this study.

The 'barrier effect distance' was estimated at *c.* 40 km [$\Delta Nm = 5.05 = 3.177 \times \log$('barrier effect' in km)]. Genetic diversity was negatively correlated with both measures of population isolation (isolation$_{\text{distance}}$ and isolation$_{\text{distance+barriers}}$) (Fig. 3). However, using isolation$_{\text{distance+barriers}}$ significantly improved regression model fit for A (Table 1; Fig. 3), indicating that the presence of barriers reduced nuclear genetic diversity. The estimated decline in A for populations isolated by barriers from all three of the nearest populations was as high as 15%. Results for mtDNA haplotype diversity were more equivocal: although isolation$_{\text{distance+barriers}}$ had a better model fit than isolation$_{\text{distance+barriers}}$ as assessed by model F-statistic significance and R^2, and greater likelihood as assessed by AIC$_c$weight, the difference was not enough to clearly indicate that isolation$_{\text{distance+barriers}}$ was the best model (Table 1). Fits of both models for mtDNA haplotype diversity were poor ($R^2 < 0.20$), suggesting that neither model was adequate. Genetic diversity (nuclear and mitochondrial) was not correlated with population area or current estimated population size (Table 1).

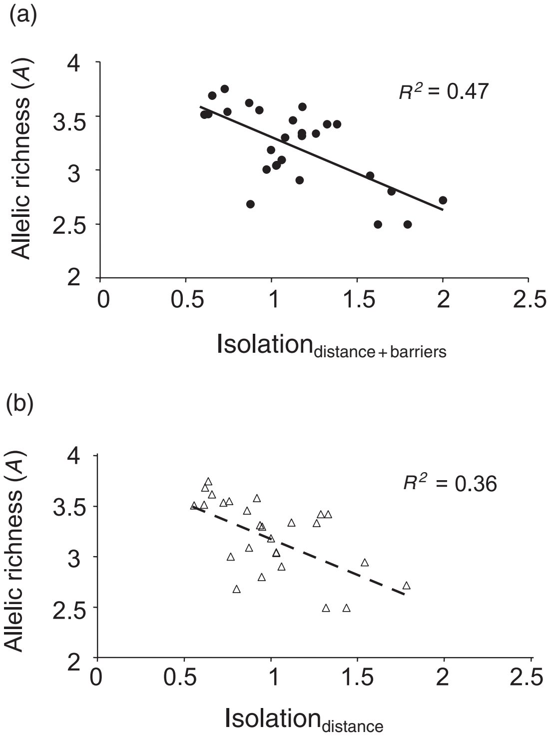

Figure 3 Regressions of allelic richness (A) on isolation as a function of distance and barriers (a) or distance alone (b). Isolation measures are based on log-transformed distances in km (see text).

The amount of gene flow among populations was strongly and negatively correlated with barriers at interpopulation distances of < 15 km (Mantel $r = -0.49$, $P = 0.0002$). When the effect of barriers was removed by partial correlation, Nm was strongly correlated among populations within 15 km (Mantel $r = 0.82$, $P = 0.0002$), weakly correlated among populations 15–30 km apart (Mantel $r = 0.16$, $P = 0.0448$), and not correlated among populations separated by greater distances. Plotting Nm as a function of distance also showed that Nm decreased sharply with distance for population pairs not separated by barriers (Fig. 2). Population pairs separated by barriers showed very low Nm values regardless of distance, suggesting that no exchange of individuals occurred across barriers (Fig. 2).

Partial correlations of pairwise F_{ST} values (genetic differentiation; Appendix S3) with barriers and distance showed a similar but weaker pattern. F_{ST} was positively correlated with the presence of barriers at interpopulation distances of < 15 km (Mantel $r = 0.168$, $P = 0.0220$) and 15–30 km (Mantel $r = 0.145$, $P = 0.0446$). F_{ST} was negatively correlated with the presence of populations within 15 km (Mantel $r = -0.444$, $P = 0.0002$), less strongly so at 15–30 km (Mantel $r = -0.174$, $P = 0.0264$), and not significantly correlated at greater distances. Because effects for both factors were detected in the first two distance classes, we also examined them across a 0–30-km distance class: F_{ST} was positively correlated with the presence of barriers (Mantel $r = 0.212$, $P = 0.0034$) and negatively correlated with the presence of populations within 30 km (Mantel $r = -0.441$, $P = 0.0002$).

Simulated datasets revealed that an increase in genetic distance (F_{ST}) because of barriers could be detected within the time frame of the age of the barriers in this study (*c.* 40 years). However, the increase in F_{ST} (0.012–0.018 depending on the parameter values used, Table 2) was not as large as the estimated increase in F_{ST} because of barriers for the actual study populations. The model of two simulated populations, 5 km apart with no intervening barrier, had an average F_{ST} ranging from 0.007 to 0.048 across the parameter set ($F_{\text{ST}} = 0.039$ between the study populations from which parameters were derived). Average F_{ST} between two simulated populations with a barrier present during the most recent seven generations increased for all parameter combinations; the increase did not appear to be greatly sensitive to the different values of Nm and θ

Table 1 Regression models of genetic diversity (corrected for sample size) as a function of human-made barriers, distance and other variables for $n = 27$ populations of desert bighorn sheep

Response variable	Model	P-value†	R^2‡	k§	ΔAIC_c	w_i¶
Allelic richness (corrected)	Log (isolation$_{\text{distance+barriers}}$)*	< 0.0001	0.47	3	0	0.88
	Log (isolation$_{\text{distance}}$)	0.0010	0.36	3	5.01	0.07
	Log (isolation$_{\text{distance}}$), population area	0.0031	0.38	4	6.96	0.03
	Log (isolation$_{\text{distance}}$), population size	0.0048	0.36	4	7.90	0.02
Number of mtDNA haplotypes (corrected)	Isolation$_{\text{distance+barriers}}$*	0.0388	0.16	3	0	0.63
	Isolation$_{\text{distance}}$*	0.0754	0.12	3	1.22	0.34
	Isolation$_{\text{distance}}$, population area, population size	0.3035	0.14	5	6.33	0.03

Model selection was performed using Akaike's Information Criterion (AIC)$_c$: models with lowest AIC$_c$ values are best fit, but models within two ΔAIC$_c$ units of the best model are considered equally explanatory. AIC weights (w_i) may be interpreted as the likelihood that the given model is the best of the candidate models (Burnham & Anderson 1998).

*Best-fit or competing model (within two AIC$_c$ units).

†Significance of model F-statistic.

‡Fit of linear regression model.

§Number of predictor variables + 2 for calculating AIC$_c$.

¶AIC$_c$ weight.

Table 2 Increases in average F_{ST} (with standard error) because of elimination of gene flow by a barrier for seven generations between two simulated populations (based on 1000 simulations)

θ	$Nm = 2$	$Nm = 6.2$	$Nm = 10$
1.00	0.015 (0.002)	0.012 (0.003)	0.013 (0.003)
3.27	0.018 (0.005)	0.015 (0.003)*	0.013 (0.003)
8.97	0.013 (0.004)	0.014 (0.002)†	0.012 (0.002)

*Nm calculated from observed F_{ST}, θ estimated from observed heterozygosity.

†Nm calculated from observed F_{ST}, θ estimated from variance in allele size.

that we employed (Table 2). However, the relative increase was sensitive to Nm and θ, in that low values of Nm increased average F_{ST} values between populations but not the difference caused by barriers. Estimated F_{ST} between the actual study populations, 5 km apart with an intervening barrier, increased from 0.046 to 0.113. This estimated increase was based on the regression equations of F_{ST} on distance for population pairs without barriers [$F_{ST} = -0.029 + 0.108 \times \log(\text{geographic distance in km})$] and for population pairs with intervening barriers [$F_{ST} = 0.080 + 0.048 \times \log(\text{geographic distance in km})$].

DISCUSSION

Nuclear genetic diversity of desert bighorn sheep populations was negatively correlated with the presence of human-made barriers that blocked dispersal to nearby populations (Table 1; Fig. 3). This finding strongly suggests that these barriers have reduced genetic diversity for many of these populations. We estimate from our results that nuclear genetic diversity in populations completely isolated by human-made barriers has declined as much as 15% in the *c.* 40 years since most barriers were erected. This estimate implies that the rate of loss of genetic diversity in populations isolated by barriers was *c.* 0.4% per year; if this rate is constant, some populations may lose up to 40% of their pre-barrier genetic diversity in the next 60 years. Results for mtDNA markers were consistent with these findings, but did not clearly support the reduction of mitochondrial genetic diversity because of barriers. The low correlation of mtDNA diversity with either distance and barriers may reflect very low dispersal rates for female bighorn sheep, as suggested by Festa-Bianchet (1991) and Jorgenson *et al.* (1997). More probably, the ambiguous results for mtDNA may reflect the stochasiticity inherent in one genetic locus (as represented by the mtDNA genome) when compared with the results derived from 14 microsatellite loci.

We believe that genetic diversity declined so rapidly after isolation because N_e of each population was likely very small. Therefore, unless diversity was maintained by gene flow from other populations, genetic drift quickly eliminated diversity. Our analyses of gene flow based on regression and partial correlation of Nm and F_{ST} with barriers and distance showed that, where present, human-made barriers have essentially eliminated dispersal (Fig. 2). The suppression of migration by barriers was most detectable within the distances at which high relative gene flow was most detectable, in this case, at < 15 km. Populations < 15 km from other populations maintained higher genetic diversity unless a human-made barrier intervened.

Finally, genetic simulations demonstrated that barriers constructed only 40 years ago could create a detectable increase in genetic distance between populations, although the increase in genetic distance in the simulations was not as great as that observed. This discrepancy may have resulted from a variety of factors. For one, these simple simulations considered only two populations. Actual populations experienced gene flow from other nearby populations, and probably experienced strong fluctuations in population sizes (perhaps caused by strong environmental stochasticity), founder effects, and other demographic events not included in the simulations that may have increased genetic distances. Thus parameter estimates (based on equilibrium conditions) for these simulations may not have been correct, although simulations with varied parameter estimates showed similar increases in genetic distance because of barriers. Historical census data (Torres *et al.* 1994), tiny population sizes and frequent recent extinctions of populations of desert bighorn sheep in California (Epps *et al.* 2004) suggest that fluctuations and founder effects have been common in the decades since the barriers have been constructed. Such metapopulation dynamics may further explain why barriers had such a strong effect on genetic diversity and genetic distance in only *c.* 40 years; this question bears further investigation with more realistic models. However, the detectable differences that our simple simulations yielded support our inference that observed patterns of genetic diversity could be due to the effects of human erected barriers (i.e. occur over such short-time frame).

Because our analyses rely on correlation of the presence of barriers with decreased genetic diversity and increased genetic distance, we cannot exclude the possibility that the genetic structure apparently created by barriers is an artifact of historical genetic structure. However, no other biogeographical explanation for such structure is readily apparent. While it is possible that roads may be constructed preferentially in flat areas or valleys between mountain ranges, nearly all of the populations considered are topographically isolated by flat areas, regardless of the presence of barriers (Fig. 1). Distance thus appears to be the prevailing natural barrier in this system, as evidenced by the strong correlation of genetic diversity and gene flow with distance, and was included explicitly in this analysis. Non-equilibrium conditions may have also affected estimates of genetic distance and other analyses. Despite this, the large number of populations considered and the consistent relationships between genetic diversity, genetic distance and the presence of barriers suggest that these findings are robust.

Our analyses point to the conclusion that human-made barriers may greatly reduce stability of the system as a whole: populations are small and re-colonization of extinct habitat patches is critical for metapopulation persistence (Hanski & Gilpin 1997; Gonzalez *et al.* 1998). Extinction risk for many desert bighorn sheep populations in California is high, and may sharply increase in the coming century because of climate warming (Epps *et al.* 2004). If movement corridors from climatically stable refugia (high-elevation ranges in this case) to more ephemeral patches are severed, re-colonization or demographic 'rescue' will be unlikely to occur. Moreover, connectivity is critical to maintain genetic diversity over the whole metapopulation. Even though strong genetic drift may rapidly remove genetic diversity from individual populations in a functioning metapopulation, this loss can be off-set by gene flow from other populations. However, if barriers disrupt gene flow and recolonization, genetic diversity may be lost very rapidly from the system as a whole (given that the total number of populations in this instance is not large). Thus barriers can have severe consequences both for demographic and genetic processes in metapopulations and may increase the danger of metapopulation extinction.

We recommend that consideration be given to ways to mitigate existing human-made barriers, and that any future construction of major highways in desert bighorn habitat should be designed to minimize disruption of connectivity. Drainage tunnels under interstate highways already exist in some areas (e.g. under Interstate 40 between the Marble and Granite mountains); while presumably large enough to allow traversal by bighorn sheep, these tunnels are within the fenced interstate corridor. Underpasses and overpasses have been used successfully to aid dispersal of carnivores and ungulates (Foster & Humphrey 1995; Gloyne & Clevenger 2001). Changes in fencing could allow access to tunnels while still preventing livestock or wildlife from entering the highway corridor itself. Overpasses could be another, perhaps more effective means of reestablishing connectivity for bighorn sheep, although the cost of such structures could be very high.

As the human population continues to expand, the need to maintain connectivity of natural populations is even greater. Rapid development of highways and other barriers has reduced and fragmented habitat for many species, while global climate change is increasing local extinction rates and forcing latitudinal or elevational shifts in species' distributions (Walther *et al.* 2002). Species-specific solutions to restoring habitat connectivity both in previously fragmented landscapes and relative to future development must be implemented.

ACKNOWLEDGEMENTS

We thank T. Anderson, J. Andre, N. Andrew, J. Ashdown, W. Baczkowski, V. Bleich, J. Brashares, B. Campbell, J. Davis, R. Dodd, M. Fan, C. Gallinger, B. Gonzales, L. Kimura, L. Lessicka, J. Novembre, A. Pauli, M. B. Rew,

J. Sexton, G. Sudmeier, S. Torres, R. Tran, D. Weaver and G. Weiss for their assistance. This research was supported by the National Science Foundation Graduate Fellowship (C.W.E.), the Bighorn Global Warming Project funded by the Agricultural Experiment Station of California, the Golden Gate Chapter of Safari Club International, the Resources Assessment Program of California Department of Fish and Game and Sigma Xi. We also thank M. Festa-Bianchet, T. Lenormand and three anonymous referees for their insightful comments on this manuscript.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from http://www.Blackwell-Synergy.com:

Appendix S1 (a) Zinc-finger gene primers and protocol, (b) microsatellite analysis protocols and references, and (c) mitochondrial DNA sequencing protocols.

Appendix S2 Sample sizes for analyses of microsatellite genotypes and mtDNA sequences, and basic genetic and geographical statistics for the 27 populations of desert bighorn sheep used in this study.

Appendix S3 F_{ST} values for all sampled populations, estimated from 14 microsatellite loci using GENEPOP.

Editor, Thomas Lenormand
Manuscript received 28 March 2005
First decision made 4 May 2005
Second decision made 30 May 2005
Manuscript accepted 10 June 2005

Appendix 1-a Zinc-finger gene primers and protocol.

We used the following primers, designed by R. Ramey, to screen for and remove weakly-amplifying extractions: ZFYf2 5'-3' TTA CTG AAT CGC CAC CTT TTG GC and ZFYr1 5'-3' CTG CAG ACC TAT ATT CGC AGT ACT (annealing temperature 57°; same experimental conditions employed for microsatellite analyses in Wehausen et al. (2004)).

Appendix 1-b Microsatellite analysis protocols and references.

Experimental conditions and references for 11 of the 14 dinucleotide microsatellite loci used in this study were described previously (Wehausen *et al.* 2004); we used the additional loci OarFCB128 and OarFCB266 (Buchanan & Crawford 1993) (annealing temperature 57°) and D5S2 (Steffen *et al.* 1993) (annealing temperature 55°). Amplification products were visualized using an ABI Prism™ 377 (Applied Biosystem Inc., Foster City, USA); alleles were designated using GeneScan™ (version 3.7, Applied Biosystem Inc., Foster City, USA) and Genotyper™ (version 3.7 NT, Applied Biosystem Inc., Foster City, USA).

Appendix 1-c Mitochondrial DNA sequencing protocols.

For mtDNA sequencing, we used ABI Prism™ 377 and 3730 sequencers (Applied Biosystems, Inc., Foster City, USA) and the following primers designed by R. Ramey: L15712 5'-3' AAC CTC CCT AAG ACT CAA GG and BETH 5'-3' ATG GCC CTG

AAG AAA GAA CC. We used 20 µL PCR reactions with the following reaction conditions: 1x PCR Buffer I (Applied BioSystems Inc., Foster City, USA), 0.16 mM dNTPs, 10 µg bovine serum albumin (New England BioLabs, Beverly, USA), 1.9 mM $MgCl_2$, 400 nM each primer, 0.8 units of Amplitaq Gold DNA polymerase (Applied BioSystems Inc., Foster City, USA), and 1 µL of extracted DNA. We used an initial heating cycle of 94º C for 7 minutes 30 seconds, followed by 35 cycles of 94º C for 60 seconds, 61º C for 70 seconds, and 72º C for 90 seconds. We cleaned PCR reactions using 0.2 units of shrimp alkaline phospatase (USB, Cleveland, USA) and 2 units of Exo I (New England Biolabs, Beverly, USA) to clean 1 µL of amplified DNA. We cycle-sequenced with BigDye™ v3.1 (Applied Biosystem Inc., Foster City, USA) following standard protocols.

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Appendix 2 Sample sizes for analyses of microsatellite genotypes and mtDNA sequences (if different, noted parenthetically) and basic genetic and geographic statistics for the 27 populations of desert bighorn sheep used in this study. $\textit{Isolation}_{\mathrm{DISTANCE}}$ is the harmonic mean of the distances to the nearest three populations; $\textit{Isolation}_{\mathrm{DISTANCE+BARRIERS}}$ adds the "barrier effect distance" of 40 km to inter-population distances if a barrier intervened (see text).

Population	$^{*}n$	$^{\dagger}H_e$	Total alleles	$^{\ddagger}A$	$^{\S}N_{\mathrm{HAP}}$	$^{\P}N_{\mathrm{HAP}}$ (corrected)	$\textit{Isolation}_{\mathrm{DISTANCE}}$ (km)	$\textit{Isolation}_{\mathrm{DISTANCE+BARRIERS}}$ (km)
Clark	12	0.614	57	3.52	2	1.92	4.1	4.3
Clipper	16	0.647	54	3.31	4	3.30	8.6	15.1
Coxcomb	7	0.622	51	3.46	3	2.86	7.3	13.5
Cushenbury	15	0.489	38	2.49	1	1	20.8	62.6
Chemehuevi	9	0.571	51	2.94	1	1	34.8	37.8
Eagle-Buzzard Spr.	17	0.653	61	3.68	1	1	4.2	4.5
Eagle-Lost Palms	14	0.627	62	3.75	3	2.31	4.4	5.3
Granite	21	0.627	66	3.62	6	3.52	4.6	7.5
Hackberry	13	0.637	49	3.18	1	1	10.0	10.0
Iron	11	0.537	43	2.68	2	1.51	6.4	7.6

Cady	12	0.591	53	3.34	4	3.28	13.2	15.1
Little San Bernardino	12	0.626	57	3.58	3	2.34	8.3	15.2
Marble	29 (28)	0.644	61	3.55	3	1.77	5.8	8.5
Newberry	15	0.496	37	2.49	2	1.93	27.2	42.0
Old Dad	25	0.561	51	3.04	3	2.75	10.7	10.7
Indian Spring	12	0.475	48	2.90	3	2.06	11.5	14.7
Orocopia	18	0.568	47	3.00	3	1.97	5.9	9.4
Old Woman	26	0.512	54	3.04	3	2.39	10.8	10.8
Piute Range	13	0.627	55	3.42	3	2.68	21.3	21.3
Providence	20	0.628	59	3.51	5	3.37	3.6	4.1
Queen	11	0.594	55	3.42	3	2.49	19.4	24.4
Riverside Granite	10 (8)	0.609	47	3.09	2	2.00	7.5	11.5
South Bristol	14	0.599	51	3.29	2	1.98	8.9	12.1

San Gorgonio	17	0.539	44	2.80	1	1	8.9	50.3
San Gabriel	6	0.549	38	2.71	1	1	60.6	101.8
Turtle	14	0.635	54	3.33	2	1.43	18.3	18.3
Wood	10	0.622	55	3.53	3	2.49	5.3	5.6

[*] number of individuals sampled per population

[†] expected heterozygosity

[‡] allelic richness corrected for variation in sample size

[§] number of mtDNA haplotypes detected

[¶] number of mtDNA haplotypes corrected for variation in sample size

Appendix 3 F_{ST} values for all sampled populations, estimated from 14 microsatellite loci using GENEPOP. All values were significantly different ($p<0.05$). Population names are abbreviated but are presented in the same order as in Appendix 2.

	CL	CO	CU	CV	EABZ	EALP	GR	HA	IR	KD	LS	MA	NE	OD	OE	OR	OW	PI	PR	QU	RG	SB	SG	SL	TU	WO
CK	0.13	0.14	0.29	0.16	0.10	0.11	0.09	0.11	0.21	0.15	0.13	0.14	0.25	0.15	0.20	0.15	0.18	0.09	0.12	0.13	0.12	0.15	0.21	0.15	0.14	0.10
CL		0.15	0.24	0.18	0.10	0.10	0.08	0.14	0.21	0.13	0.13	0.05	0.20	0.15	0.19	0.18	0.17	0.12	0.11	0.15	0.11	0.07	0.20	0.20	0.16	0.13
CO			0.27	0.16	0.11	0.07	0.07	0.10	0.16	0.10	0.10	0.14	0.26	0.06	0.20	0.19	0.12	0.11	0.10	0.09	0.10	0.15	0.16	0.22	0.16	0.06
CU				0.35	0.18	0.18	0.20	0.31	0.26	0.28	0.20	0.25	0.37	0.27	0.32	0.29	0.22	0.26	0.27	0.23	0.22	0.24	0.07	0.37	0.31	0.26
CV					0.21	0.21	0.12	0.15	0.29	0.18	0.24	0.18	0.33	0.18	0.24	0.25	0.22	0.16	0.19	0.22	0.20	0.19	0.27	0.26	0.22	0.14
EABZ						0.02	0.07	0.13	0.17	0.14	0.04	0.13	0.25	0.15	0.19	0.15	0.13	0.10	0.09	0.06	0.07	0.12	0.12	0.21	0.13	0.12
EALP							0.06	0.12	0.13	0.13	0.04	0.12	0.23	0.11	0.18	0.16	0.10	0.10	0.08	0.03	0.07	0.10	0.12	0.20	0.12	0.09
GR								0.06	0.17	0.11	0.08	0.10	0.18	0.09	0.13	0.17	0.12	0.08	0.05	0.11	0.08	0.11	0.13	0.17	0.13	0.05
HA									0.21	0.14	0.13	0.13	0.21	0.14	0.19	0.22	0.18	0.08	0.06	0.16	0.17	0.16	0.21	0.17	0.18	0.02
IR										0.24	0.18	0.21	0.32	0.19	0.29	0.29	0.05	0.19	0.18	0.14	0.17	0.23	0.19	0.21	0.21	0.19
KD											0.15	0.09	0.26	0.11	0.10	0.17	0.17	0.12	0.15	0.16	0.12	0.12	0.20	0.21	0.18	0.12
LS												0.14	0.24	0.16	0.21	0.17	0.13	0.12	0.12	0.05	0.11	0.14	0.15	0.22	0.13	0.13
MA													0.14	0.16	0.18	0.17	0.15	0.10	0.11	0.16	0.12	0.04	0.19	0.20	0.15	0.13
NE														0.27	0.35	0.30	0.26	0.15	0.19	0.25	0.28	0.19	0.27	0.32	0.25	0.24
OD															0.10	0.23	0.16	0.13	0.11	0.17	0.15	0.15	0.18	0.21	0.20	0.11
OE																0.26	0.20	0.19	0.18	0.22	0.21	0.20	0.24	0.24	0.26	0.17
OR																	0.23	0.20	0.22	0.13	0.15	0.16	0.24	0.25	0.20	0.22
OW																		0.14	0.15	0.10	0.11	0.17	0.16	0.18	0.15	0.16
PI																			0.07	0.13	0.12	0.12	0.16	0.17	0.09	0.05
PR																				0.13	0.15	0.14	0.17	0.18	0.15	0.05
QU																					0.09	0.14	0.16	0.21	0.15	0.15
RG																						0.13	0.16	0.22	0.13	0.13
SB																							0.20	0.23	0.18	0.14
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POINTS OF VIEW: A CONTROVERSY IN CONSERVATION BIOLOGY

EDITOR'S NOTE.—The following three papers constitute an essay by C. K. Dodd, Jr. and R. A. Seigel followed by two replies to the essay by, respectively, R. L. Burke and H. K. Reinert.

Herpetologica, 47(3), 1991, 336–350

RELOCATION, REPATRIATION, AND TRANSLOCATION OF AMPHIBIANS AND REPTILES: ARE THEY CONSERVATION STRATEGIES THAT WORK?

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ABSTRACT: Conservation strategies involving relocations, repatriations, and translocations (RRT) have been carried out, are underway, or are advocated for a number of endangered and threatened amphibians and reptiles. However, recent reviews of RRT projects involving birds and mammals suggest that the success rate is low and that the factors that lead to endangerment operate to impede effective RRT results. In this paper, we review available information on RRT projects involving amphibians and reptiles, examine the motives for advocating RRT strategies, and recommend biological and management criteria that should be considered prior to undertaking RRT projects. Most RRT projects involving amphibians and reptiles have not demonstrated success as conservation techniques and should not be advocated as if they are acceptable management and mitigation practices. We urge caution in accepting claims of success and urge colleagues to publish detailed methods and results of past and ongoing RRT projects.

Key words: Amphibians; Reptiles; Repatriation; Relocation; Translocation; Conservation; Management

THE concept of re-establishing populations of endangered or threatened species in areas where they have been extirpated has become extremely popular in recent years. For example, Griffith et al. (1989) reported that approximately 700 translocations or repatriations occurred each year, mainly in the United States and Canada. Variously termed "reintroductions", "translocations", and "repatriations", such programs have the laudable goal of reducing the probability of extinction by increasing the number of viable populations or increasing the number of individuals in small populations (Campbell, 1980; Scott and Carpenter, 1987). Repatriations into natural habitats are frequently combined with captive-breeding programs at zoological parks (Scott and Carpenter, 1987) and may spark wide public interest.

Despite the increasing popularity of repatriation programs as a conservation technique, serious questions have arisen about the theory behind such programs and their effectiveness (British Herpetological Society, 1983; Campbell, 1980; Conant, 1988; Griffith et al., 1989; Mlot, 1989; Scott and Carpenter, 1987; Tasse, 1989). In a comprehensive review of the success of repatriation and translocation programs for birds and mammals, Griffith et al. (1989) found an overall project success rate

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f 44%. They noted that success rates were pparently dependent on a variety of ecological factors, including the quality of the habitat where the release occurred, whether the individuals released were wild or captive-bred, and the feeding habits of adults.

There has been considerable recent interest in the conservation of reptiles and mphibians despite the fact that they lack he broad public appeal of birds and mamnals. In the United States, Puerto Rico, and the U.S. Virgin Islands, 11 species of amphibians and 29 species of reptiles are currently on the federal list of Endangered and Threatened Wildlife and Plants, with many other species protected by state and territorial regulations. Frequently, management, conservation, and recovery plans or endangered or threatened reptiles and mphibians involve repatriation, relocaion, or translocation (hereafter referred to as RRT) programs. Such programs often become highly visible and intertwined with local political concerns. For example, relocation programs for the gopher tortoise (*Gopherus polyphemus*) have been used as mitigation allowing development of uplands habitats throughout Florida. Given he extremely limited resources (both in ime and money) available for conservation programs for reptiles and amphibians, a detailed understanding of the effectiveness of repatriations or translocations is essential (Scott and Carpenter, 1987). However, we are unaware of any critical review of the success of repatriation or translocation programs for amphibians and reptiles. In this paper, we provide such a reiew.

DEFINITIONS

A wide variety of terms have been used to refer to programs where animals are released into areas where they have become extirpated or rare (British Herpetological Society, 1983; Conant, 1988; Griffith et al., 1989; Mlot, 1989; Scott and Carpenter, 1987; Tasse, 1989). For the urposes of this paper, we define the rease of individuals of a species into an area ormally or currently occupied by that species as a repatriation, whereas releases of individuals into geographic areas not historically occupied by that species are termed translocations. Relocation involves moving an animal or population of animals away from an area where they are immediately threatened (e.g., by development) to an area where they would be less prone to habitat loss; ideally, relocated animals should be moved to habitats where they historically occurred, but this is not always the case.

There is considerable confusion in the literature concerning what the term "success" means in the context of repatriation or translocation programs. Because the goal of any conservation program is the establishment (or enhancement) of a viable, self-sustaining population, we follow Griffith et al. (1989) in defining a repatriation, relocation, or translocation as successful only if evidence is presented that a self-sustaining population has been established. Hence, the presence of some breeding individuals does not, in our opinion, constitute evidence for success unless it can be shown that the population is at least stable. Because many endangered reptiles and amphibians have long life spans (e.g., sea turtles, tortoises), determining the success of a given release may be difficult and time-consuming. Nonetheless, we suggest that the burden of proof is on the investigator to show that a self-sustaining population exists before declaring success; to do otherwise would be to imply that the probability for extinction has been lowered for that species, when, in fact, this may not be true.

Our review is based on published references in the open literature, unpublished references (often in the form of reports to various resource management agencies), and personal communications solicited from colleagues. We recognize that we may have missed RRT programs whose results remain unpublished.

DISCUSSION OF RRT PROGRAMS

We documented RRT programs that had been carried out for 25 species of amphibians and reptiles (Table 1). We consider the RRT programs for *Chelonia mydas* separately, but combine RRT programs

TABLE 1.—Tabulation of actual and planned RRT projects involving amphibians and reptiles. U = unknown, E = eggs, L = larvae, J = juveniles, H = hatchlings, A = adults, N = not successful, C = casual observations. Reasons for relocation failure as follows: 1 = unknown, 2 = unsuitable habitat, 3 = unsuitable developmental conditions, 4 = human predation, 5 = animals moved away from release site, 6 = mongoose predation, 7 = poor release design.

Species	Location	Stage	Success	Reproduction	Follow-up	Reference
RRT projects completed or in progress						
Amphibians						
Salamanders						
Plethodontidae						
Plethodon idahoensis	Montana	A?	U(2, 7)		U	Anon (1990)
Salamandridae						
Triturus vittatus	USSR	J	U	Y	Y	Goncharov et al. (1989)
Frogs						
Bufonidae						
Bufo calamita	England	L, U	N(1)		U	Beebee (1983); Corbett (1989)
Peltophryne lemur	Puerto Rico	J, A	U		C	Miller (1985); Paine and Duval (1985); Paine et al. (1989); Paine (personal communication)
Pelobatidae						
Pelobates syriacus	USSR	L, J	U	Y	Y	Goncharov et al. (1989)
Reptiles						
Turtles						
Cheloniidae						
Caretta caretta	Virginia	E	N(1, 3)	N	C	Dodd (1988*a*)
Chelonia mydas	Caribbean	H	N(1)	N	N	Carr (1984); Dodd (1982); Huff (1989); Parsons (1962)
	Florida	H	U	U	C	
Lepidochelys kempi	Texas	E	U	N	Y	Caillouet and Landry (1989)
Chelydridae						
Macroclemys temmincki	Georgia	H	U	U	U	Pritchard (1989)
Testudinidae						
Geochelone elephantopus	Galapagos Is.	J	U	Y	U	MacFarland et al. (1974); Bacon and Reynolds (1982); Snell (personal communication)
G. gigantea	Seychelles	A	U(4)	Y	Y	Stoddart et al. (1982); Samour et al. (1987); Spratt (1989)
Gopherus polyphemus	Southeast USA	A	U(1, 2, 4, 5)	Y	Y, N, U	Bard (1989); Burke (1987, 1989*a*,*b*); Diemer (1986, 1987, 1989); Dietlein and Smith (1979); Doonan (1986); FGFWFC (1989); Fucigna and Nickerson (1989); Godley (1989); Layne (1989); Lohoefener and Lohmeier (1986); Stout et al. (1989)
Xerobates agassizi	California	A	N(1, 5)		Y, C	Berry (1986); Cook (1983); Cook et al. (1978); St. Ame[illegible] Hoover (1980); Web[illegible] (1979)

Stout et al. (1989)

Xerobates agassizi	California	A	N(1, 5)		Y, C	Berry (1986); Cook (1983); Cook et al. (1978); St. Amant and Hoover (1980), Weber et al (1979)

TABLE 1.—Continued.

Species	Location	Stage	Success	Reproduction	Follow-up	Reference
Lizards						
Cordylidae						
Cordylus giganteus	South Africa	U	U		U	Jacobsen et al. (1990)
Iguanidae						
Conolophus subcristatus	Galapagos Is.	U	U	Y	U	Snell (personal communication)
Cyclura pinguis	Br. Virgin Is.	U	U		U	Lazell (1989)
Lacertidae						
Lacerta agilis	England	A	Y, N, U(1, 2)	Y	Y	Corbett (1988); Spellerberg (1988); Spellerberg and House (1982)
Teiidae						
Ameiva polops	US Virgin Is.	A	N(6)	N	C	Dodd (1978)
Snakes						
Colubridae						
Drymarchon corais	Southeast US	A, J	U(1)		U	Smith (1987); Speake et al. (1987)
Crocodiles						
Crocodylidae						
Alligator mississippiensis	Arkansas	U	Y	Y	C?	Joanen and McNeese (1990)
Crocodylus niloticus	Nigeria	A	U		N	Morgan-Davies (1980)
C. palustris	India	J	Y		Y?	Choudhury and Bustard (1982)
C. porosus	India	H	Y		Y	Choudhury and Chowdhury (1986)
Gavialidae						
Gavialis gangeticus	India	J, H	Y	Y	Y	deVos (1984); Choudhury and Chowdhury (1986); Rao (1990)
Planned or proposed RRT projects						
Amphibians						
Plethodontidae						
Batrachoseps aridus	California					USFWS (1982)
Bufonidae						
Bufo hemiophrys	Wyoming					USFWS (1990*a*)
Discoglossidae						
Alytes muletensis	Mallorca					Tonge (personal communication)
Reptiles						
Scincidae						
Leiolopisma telfairi	Round Is.					Bloxam (1982); Tonge (personal communication)
Teiidae						
Cnemidophorus vanzoi	St. Lucia					Tonge (personal communication)

for other species. Of these RRT projects, five (19%) were classified as successful, six (23%) were unsuccessful, and 15 (58%) could not be classified although in six instances reproduction occurred. Thus, the success rate for RRT programs for reptiles and amphibians is considerably lower than for birds and mammals (44%: Griffith et al., 1989). Moreover, the success rate for reptiles and amphibians varied phylogenetically; of the five successful programs, four involved crocodilians. If projects were considered individually rather than by species, especially for all gopher tortoise RRT's, the success rate would be lowered considerably. Although reproduction may have occurred, no RRT program has yet established a self-sustaining population of snakes, turtles, frogs, or salamanders.

We recognize that some of the cases marked as "unknown" could eventually prove to be successful, such as projects involving the Aldabra and Galapagos tortoises and Galapagos land iguana. We also note that some of the cases currently listed as successful are based on limited follow-up data, and long-term studies could show that initial optimism was premature. There are few published accounts dealing with the rationale, methodology, results, and criteria for success of conservation-related repatriation, relocation, or translocation projects (but see Stubbs, 1989).

Examples of RRT Projects

In the following section, we summarize data on several representative RRT activities. While space limitations preclude a detailed summary of each actual or proposed RRT project listed in Table 1, a summary can be obtained by contacting the authors.

Bufo houstonensis.—Conservation efforts for the Houston toad have involved extensive data collection on both natural populations and the husbandry of toads in captivity. The project was begun in 1978 by the Houston Zoo to identify remaining populations and to either supplement existing populations or to start new populations in protected areas using wild adults, naturally deposited eggs, or captive-reared juveniles and adults. Ten sites at Attwater Prairie Chicken National Wildlife Refuge (APCNWR) were chosen in 1982 for introduction, and tadpoles or juveniles were observed 6 wk after the 1982 and 1 releases. Detailed descriptions of husbandry, sites, release methods and numbers, and monitoring are contained in unpublished reports to the U.S. Fish and Wildlife Service (Quinn, 1980, 1981; Quinn and Ferguson, 1983; Quinn et al., 1984). However, despite careful laboratory and field techniques and the introduction of 0.5 million individuals since 1982 (adults, juven recent metamorphs, tadpoles), not even a new population of the Houston toad has been successfully established at APCNWR (H. Quinn, personal communication).

Lepidochelys kempi.—From 1978 through 1988, freshly deposited Kemp's ridley eggs (1000–3000/yr) were transported from Rancho Nuevo, Mexico, to Texas in an attempt to establish a new nesting colony on protected Texas beach Eggs were incubated in sand at Padre land and hatchlings were allowed to enter the water at Padre Island National Seashore to allow for possible imprinting on environmental cues. Hatchlings were then shipped to a National Marine Fisheries Service rearing facility at Galveston for head-starting. More than 17,000 hatchlings were imprinted at Padre Island, an >12,000 turtles have been released aft head-starting. Details of the project, including rationale and objectives, methodology of transport, rearing, and release, numbers of turtles involved, and mortality and disease, have been outlined in a popular book (Phillips, 1989) and discussed by many papers in a symposium volume edited by Caillouet et al. (1989). The Padre Island phase of the Kemp's ridley project was terminated after the 1988 season.

Gopherus polyphemus.—The most numerous and extensive relocations and translocations of any amphibian or reptile species involve the gopher tortoise in the southeastern United States. Although thousands of animals have been moved from one area to another, particularly within Florida, in efforts to mitigate development or mining of the tortoise's remaining habitat, few details are available

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d these relate to only a few projects ard, 1989; Burke, 1987, 1989*b*; Diemer, 1986, 1987, 1989; Doonan, 1986; Fucigna and Nickerson, 1989; Stout et al., 1989). Additional animals have been released into populations from which they did not originate after use in tortoise races (e.g., Dietlein and Smith, 1979), although this practice now has ceased. Other efforts have ought to establish populations in areas that ay be outside the historic range (e.g., in e Fall Line Hills of Alabama), in isolated locations at the limits of the species' range (e.g., in Tangipahoa Parish, Louisiana), or in reclaimed phosphate mines (Godley, 1989).

Diemer (1989) reviewed relocations of gopher tortoises that occurred in Florida prior to 1987. Details were provided on ine additional relocations at a 1987 symosium sponsored by the Florida Game nd Fresh Water Fish Commission (Burke, 1989*b*; Fucigna and Nickerson, 1989; Godley, 1989; Layne, 1989; Stout et al., 1989). Four studies followed tortoises 2 yr or less. Each of the four short-term relocations involved moving a group of tortoises from one or more sites to one or more different sites. Generally about 50% of relocated tortoises remained within 0.5 km 1 yr after lease.

Additional details are available from two studies reported at the 1987 symposium. Burke (1987, 1989*b*) reported that 35 of 85 relocated tortoises in south Florida remained 2 yr after relocation, an "apparently stable population". Although his study was of short duration, Burke (1989*b*) concluded that tortoises could be relocated "fairly successfully" and that his work did t support social factors as influencing ccess rate. In a central Florida relocation Bard, 1989; Doonan, 1986), two of 12 radio-tagged tortoises could be accounted for after 41 mo while only three of 30 non radio-tagged animals were ever recaptured after release. Seven relocated tortoises were recaptured on 11 occasions compared with 144 captures of resident rtoises on 188 occasions.

Until 1990, moving tortoises from one ea to another was accepted as a conflict mitigation measure, especially for Developments of Regional Impact (DRI's), by the State of Florida, particularly in the rapidly growing central and southern regions of the state. Between 75 and 100 relocations, involving thousands of tortoises, have occurred or been authorized (D. Wood and J. Diemer, personal communication). Details concerning these relocations are unknown.

Lacerta agilis.—After a severe fire on a nature reserve in 1976, surviving sand lizards were collected. In 1978, they were moved to an outdoor vivarium. In 1981, the vivarium held a breeding colony, the purpose of which was to furnish animals for eventual reintroduction to the burned area (Spellerberg and House, 1982). Lizards were released in 1981 and recolonized the burned area. By 1988, the heathland community had recovered and sand lizards were again prevalent (Spellerberg, 1988). Details concerning follow-up sampling or lizard numbers were not presented. Other relocations and translocations of this species have occurred throughout southeastern England (primarily Dorset), and more recently in northwestern areas, for at least 20 yr. However, little information appears in the literature concerning specific details. Four populations from releases 17 yr ago continue to survive: one survives after 13 yr, two survive after 5 yr, and only two have disappeared because of fire (Corbett, 1988). A population in the Inner Hebrides continues to survive 14 yr after establishment although this area is outside the known distribution and climatic requirements for the species (Corbett, 1988).

Crocodilians in India.—Relocation efforts in India have been summarized by de Vos (1984) and Choudhury and Chowdhury (1986), including discussions of objectives, criteria for relocation, problems, and the need for monitoring the release. However, specific data on individual reintroductions and the long-term status of introduced animals is unavailable.

More than 1000 muggers (*Crocodylus palustris*) have been reintroduced in 22 locations as of 1986. As of 1986, 1022 saltwater crocodiles (*C. porosus*) had been reintroduced in India in five locations

(Choudhury and Chowdhury, 1986). Reintroduction of both species is thought to be successful.

The reintroduction of gharials (*Gavialis gangeticus*) to areas where they had been eliminated or severely reduced is touted as a major conservation achievement in India. As of 1986, 1456 gharials had been released in eight locations (Choudhury and Chowdhury, 1986). Specific details are available only for the reintroduction at the National Chambal Sanctuary where monitoring has been conducted since 1975 (Rao, 1990). In 1988, 50 nests at 15 sites were reported, and the nesting population was estimated at 50 animals (Rao, 1990). A total of 1287 captive-raised gharial have been released in the Chambal River, and the total population estimate based on 1987–1988 surveys was 804.

WHY IS MOVING ANIMALS SO POPULAR?

Because the success rate of RRT movements for conservation-related purposes is not very high, the reasons for advocating such efforts as conservation strategies should be examined. We suggest the following reasons may help to explain the advocacy of RRT movements as conservation practices, and we recommend a change in attitudes concerning these practices.

Good publicity.—Moving animals from one area to another for what promoters describe as conservation-related purposes, particularly popular species such as sea turtles and tortoises, creates favorable media attention and publicity. Media attention in turn can be used to increase the public's awareness of problems facing the species and perhaps generate funding for other less public activities such as land acquisition and basic research. However, the "30-second spot" or short newspaper story may create a false positive image for the non-involved public, affected individuals (e.g., land developers or home owners), advocacy groups, and even land managers and agency administrators. The result is a belief that such movements are a proven conservation strategy that benefits the individual animal and species. Critical examinations of relocation results and consequences are rarely part of media coverage. From a cynical point of view, positive public perception of the success of human-mediated animal movements may be desirable if alternatives are difficult to undertake or costly (see Political concerns below).

Some relocations are successful.—There have been successful conservation related RRT movements involving amphibians and reptiles (Table 1), for example, among the crocodilians and for the sand lizard in Britain. Although there is not much information in the published literature, crocodilian biologists have exchanged unpublished information on relocation and reintroduction techniques through correspondence and attendance at the meetings of the Crocodile Specialist Group of the International Union for the Conservation of Nature and Natural Resources. Likewise, conservation groups in England are closely situated to exchange information on sand lizard relocations. Exchange of information has undoubtedly facilitated the success of these efforts.

Perceived successes.—Perceived successes result from inadequate information presented to the general public, inappropriate extrapolation of results from one study to other taxa, and premature report of success.

Some individuals and organizations (e.g., Tasse, 1989) have advocated RRT movements as a conservation strategy based on limited success in a few species: for example, the Arabian oryx repatriation or the rock wallaby translocation from Australia to Hawaii. We believe such advocacy is naive and ill-informed. If two species have similar biological requirements and evolutionary history, extrapolation of the results from one taxon to the other may be initially justified. However, we do not recommend the automatic acceptance of positive results on one species as a substitute for critical experimentation and long-term monitoring of the related species. The recent publication of critical examinations of movement-related management of a wide variety of birds and mammals should serve as a caution for even within-taxon extrapolation of results (Conant, 1988; Griffith et al., 1989).

Of greater concern to us, however, is the premature claim of "success" by researchers involved with RRT movements. For instance, we fail to understand how a 50–60% desertion rate by gopher tortoises relocated in south Florida, surrounded by urban development and monitored for only 2 yr or less, can be heralded as a success and proof that relocation works (Burke, 1989*b*). Such claims give credence to the perception that RRT movements are proven management strategies that can be used to mitigate questions of habitat loss. In turn, this perception undermines efforts to protect existing habitat and appears to provide an easy way out of difficult land use questions. Until long-term studies have demonstrated otherwise, human-mediated movements of amphibians and reptiles should not be taken as proven conservation strategies, but only as experimental strategies designed to fit specific needs. Researchers should temper their claims of success with a recognition of the need for long-term evaluation. If they do not, editors should.

Lack of information on failures.—We suspect one of the most likely reasons human-mediated movements of animals for conservation purposes are continually proposed is the lack of information on what has been attempted in the past. Information on criteria for RRT movements, techniques, and results are very difficult to obtain for most studies, even those claimed as "successes". Data on negative results are virtually impossible to find. Perhaps the reasons for failure of most RRT movements are unknown. However, we consider it essential that both positive and negative results be made available in accessible sources if mistakes are to be avoided in the future.

Political concerns.—Relocation has been advocated in areas where rapid development is occurring, particularly involving tortoises in south and central Florida. Moving animals rather than killing them during construction would seem to be a humane way of dealing with problems related to habitat loss. However, most relocated or translocated animals move off the relocation or translocation site, and long-term studies have yet to demonstrate the effectiveness of these techniques. *When* the animals die becomes more important than *if* they die. In addition, commensals and other less glamorous members of the threatened community often are not considered. Rather than creating within-habitat protected areas or dealing with the larger issues of habitat protection in rapidly growing areas, relocation allows an expedient answer to a crisis demanding immediate attention. As such, relocation and translocation efforts have become the "cost of doing business" rather than well thought out strategies for effective conservation.

Humane considerations.—Concern for the fate of individual animals has sparked interest in moving them from harm's way. Concern is shown generally for the larger and more charismatic or benign reptiles, particularly tortoises, although humane reasons are sometimes used as a justification for relocating crocodilians or smaller species. Relocating animals for humane considerations can be used to foster interest in nature and involve individuals, especially young persons and the elderly, in active participation in conservation issues and activities. However, animals relocated for humane reasons should be released in accordance with the same scientific principles that guide other relocations and translocations.

Self-interest.—We have received reports that a few consultants have promoted relocation not as a measure to mitigate habitat-related conflicts, but because they want to make a large profit from the relocation. Rumors exist of consultants charging clients exorbitant fees for relocations of tortoises in south Florida (G. Dalrymple, personal communication). While we believe that most consultants operate within professional and ethical guidelines, reasons for relocating amphibians and reptiles should not be based solely on the profit to be made from the relocation. Consultants should ensure that scientific principles guide the relocation and that provisions for the long-term survival of the relocated animals are in place prior to relocation.

RECOMMENDATIONS

In addition to the recommendations we have made in the preceding text, the topics discussed below should be addressed prior to advocating or undertaking RRT projects for conservation purposes. Lack of clearly defined objectives, methodology, measures of success, and provisions for long-term follow-up studies is an indication of a project likely to fail. In addition, we cannot over-emphasize the need to publish the results of RRT experiments in appropriate journals. The methodology and results of both successful and unsuccessful RRT experiments need to be presented in detail to ensure that future efforts benefit from past experience. Unfortunately, it is our experience that seemingly obvious questions often are not asked during the planning stages of RRT projects.

Know Causes of Decline

A sound recovery plan for any species should start with a detailed understanding of what caused the species to become endangered or threatened. Consequently, RRT programs should only be attempted if (a) the causes of the original decline are reasonably well understood, and (b) those problems have been eliminated. In several cases, an understanding of why the species became endangered or threatened was not apparent (e.g., *Bufo houstonensis, Peltophryne lemur*) or was ignored (e.g., *Ameiva polops*), and these RRT programs have not been successful.

Know Biological Constraints

Although intuitively obvious, the need for RRT projects to operate within the biological constraints imposed by the species must be re-emphasized. Several projects have failed, at least in part, because of lack of attention to the biological requirements of the species (Beebee, 1983; Berry, 1986; Dodd, 1988*a*). Biological constraints to conservation are those factors that set the limits within which human-mediated actions can be taken: i.e., they comprise animal's life history requirements. Th include habitat, demographic, and bi physical components. Various authors have discussed the need to consider the biological and habitat requirements of herpetofaunal species in specific RRT projects (e.g., Bloxam, 1982; Berry, 1986; Diemer, 1989).

Habitat constraints.—We refer to habitat constraints as the physical charact istics, both macro and micro, that in ence a species' presence. These inclu sufficient space for feeding, reproduction, cover, and social interaction of all life stages; space to allow for a population sufficiently large so that environmental fluctuation and demographic stochasticity do not lead to extinction (Soulé, 1983); food of proper nutrient content and availability, especially for herbivores; habitats free fro adverse disturbance, especially from th related to human activity, roads, and pr dation or modification by introduced, feral, or domestic animals (especially dogs, cats, mongooses, pigs, and cattle); habitats designed to minimize "edge effects"; habitats without unnaturally large concentrations of natural predators, such as raccoons and ravens; and habitats free of toxic pollutants. Appropriate habitats should b available for all phases of the life cycle.

In addition to the size and disturbance factors above, the proper habitat must be available in sufficient quality. Factors to be considered include vegetative structure (e.g., important for gopher tortoises and many lizards), friable soils (for digging species), moisture requirements and access, access to dispersal agents (e.g., offshore currents for sea turtles), and acces to symbionts (e.g., bacteria to aid gut fer mentation in herbivorous species).

For wide ranging species, corridors for dispersal or migration (Harris, 1988; Harris and Gallagher, 1989) should be factored into the selection of RRT sites. Active management should be planned for RRT release sites (Griffith et al., 1989), but we caution that single species management may have detrimental effects on other sensitive species and should generally be avoided.

Demographic constraints.—Population characteristics of both the released animals and [illegible] animals already on-site, if any, should be considered prior to undertaking RRT projects. Factors include knowledge of both the age and size structure of affected animals, sex ratios, and social structure. Social structure must be considered in terms of mating system, spacing and movement patterns, and cannibalism.

Biophysical constraints.—As ectotherms, amphibians and reptiles have thermal requirements not common to endotherms. RRT projects should consider specialized biophysical requirements, especially to ensure the presence of undisturbed basking sites. Amphibians and reptiles also need a proper environment for egg development (temperature, moisture, gas exchange, waste excretion, pH, ion concentration). For species with environmental sex determination (ESD), sex ratios may be affected by the location of nest sites and season of deposition (e.g., Mrosovsky et al., 1984; Mrosovsky and Provancha, 1989; Vogt and Bull, 1984). ESD thus affects existing and future population structure. Many reptiles have ESD (Deeming and Ferguson, 1988), especially those targeted for RRT projects (crocodilians, turtles).

Unless habitat, demographic, and biophysical requirements of species are carefully considered, RRT success will be random and most likely to fail. We recommend that thorough knowledge of a species' life history requirements be a prerequisite to the adoption of RRT strategies. The lack of information on the life history of amphibians and reptiles, especially in different geographic regions, emphasizes the need for basic research.

Population Genetics and Social Structure

Conservation biologists have recently focused considerable attention on the concept of the minimum viable population size (Samson, 1983; Samson et al., 1985; Shaffer, 1981; Shaffer and Samson, 1985): the number of breeding individuals in a population needed to avoid possible deleterious effects of inbreeding and loss of genetic variability as the result of drift (Simberloff, 1988). Although the exact consequences of small population size remains unclear (Simberloff, 1988), a consideration of population genetic factors is considered to be essential to successful management (Frankel and Soulé, 1981; Lande, 1988).

The RRT programs that we reviewed, with the exception of the Puerto Rican crested toad project, did not give any consideration to population genetics when planning the repatriation or translocation. Even for *Peltophryne lemur*, studies on mitochondrial DNA began long after initial repatriation attempts. Although the exact numbers of individuals used in RRT programs often are not available, in several cases (e.g., many gopher tortoise programs), the number of individuals released is clearly much smaller that the 50–500 number frequently cited as the minimum necessary to sustain a viable breeding population (see Simberloff, 1988, for a review and critique of these numbers). In addition, because many newly-released individuals do not become part of the breeding population, the actual number of animals released may need to be much higher than the theoretical effective population size. If the planners of RRT programs rejected the idea of a minimum viable population size because of a sound theoretical argument, we would have little basis for criticism. However, to neglect the subject entirely suggests either ignorance of the consequences of small population size or wishful thinking that the project may "work out" despite the small number of individuals released.

In a similar manner, we suggest that more specific attention should be devoted to the social structure of the released group of animals based on specific information from natural populations. For example, if natural populations of a species have a characteristic sex ratio, then that sex ratio should be maintained among released animals because of its potential bearing on social interactions (e.g., dominance, hierarchies, harem formation, movements away from areas). Obviously, detailed information on the life history and population ecology of the managed species is required.

Disease Transmission

There are few studies on the effects of disease on natural populations of amphibians and reptiles. However, disease may be confined to localized populations and have serious consequences, at least on a short-term basis (e.g., Dodd, 1988*b*). Of more immediate concern is the potential for introducing disease to wild populations from either captive animals released into the wild or from moving diseased animals from one population to another.

For example, disease has proved catastrophic and led, in part, to federal protection for the desert tortoise in the western Mojave Desert (U.S. Fish and Wildlife Service, 1990*b*). The disease affects the upper respiratory tract, hence the name upper respiratory disease syndrome (URDS), and combined with nutritional problems and long-term environmental stress is nearly always fatal. Preliminary work suggests that the agent is a *Mycoplasma* (Jacobson and Gaskin, 1990) that is spread from individual to individual through direct contact. URDS is common in captive reptiles (Jacobson and Gaskin, 1990), and the locations of areas where the disease was first observed suggest that it may have been introduced to wild populations from released captives.

A similar URDS has been diagnosed in the population of *Gopherus polyphemus* on Sanibel Island, Florida, and more recently near Ft. Myers and along the Tamiami Trail. While it is premature to speculate whether the disease is identical with URDS in desert tortoises, preliminary data suggest that transmission is directly from one tortoise to another, and that the disease is highly contagious and often fatal (G. McLaughlin, personal communication). Captive tortoises are known to have been released on Sanibel Island, and it is possible that the disease was introduced by a released captive. The appearance of URDS in a wild population is cause for concern, because thousands of tortoises now are routinely relocated and translocated from one area to another within Florida.

Because of the threat of disease transmission, we recommend that health checks be adopted for animals scheduled to relocated or translocated prior to actual movement, particularly for groups such as tortoises that are known to be susceptible to contagious diseases. Release of long-term captives should always be discouraged. Health checks should include clinical evaluation using hematologic diagnosis (Rosskopf and Woerpel, 1982) by a veterinarian familiar with herpetofaunal patholo Keeping animals in a pen or "halfw house" may increase the opportunity to observe disease problems prior to release, but may expose animals to other problems including disruption of social behavior and vandalism. Individuals from an area with known disease problems, such as Sanibel Island, should never be moved to areas where they could infect wild populatio

Need for Long-term Monitoring

There is a critical lack of information on the long-term success or failure of herpetofaunal-related RRT projects even when monitoring has been incorporated into management and conservation programs. Except for the study of gopher tortoises by Layne (1989), Aldabra tortoises in the Seychelles (Table 1), and the monitoring of crocodilian repatriation projec in India, details of reputed successes, such as with sand lizards in Great Britain, are lacking.

For the other studies that we reviewed, data are either unavailable or the projects have not been monitored long enough to evaluate success or failure. We are especially critical of claims of relocation "successes" involving long-lived species where monitoring occurred for a relatively short time. For example, Burke (1989*a* claimed relocation had no effect on existing social structure of resident tortoises, and that tortoises could be successfully relocated (Burke, 1989*b*) despite data to the contrary on related species (Berry, 1986). He monitored relocated animals for only 2 yr at the end of which only 41% of the relocated tortoises remained on the release site. Monitoring a population of an animal for only 10% of the time it takes to reach

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sexual maturity hardly qualifies as enough time to measure long-term relocation "success." Likewise, we suggest that claims of success involving other tortoise relocations (e.g., Fucigna and Nickerson, 1989; Godley, 1989; Stout et al., 1989) are premature and tend to foster a false impression that relocation and translocation are proven management techniques.

Long-term monitoring of marked individuals will be required to establish the success or failure of RRT projects. What constitutes "long-term" will depend on the life-history characteristics of the species. For instance, a long-term monitoring program might continue 10–15 yr for a toad, but extend >20 yr for tortoises. Such long-term monitoring will establish not only the presence of released individuals but also the success or failure of reproduction. Long-term monitoring will ensure that release sites can maintain their integrity rather than become susceptible themselves to destruction or encroachment from "edge-effects".

We recommend that RRT projects involving amphibians and reptiles should not be attempted unless provisions are made for a biologically-based, long-term monitoring program. Considerations such as duration of monitoring that are based on non-biological priorities should not eclipse the need for evaluation within the biological constraints of the species. RRT movements should be considered experimental unless long-term studies document the feasibility of the movement on the same or a related species. Periodical evaluation is important. We caution our colleagues to exercise restraint when evaluating the "success" of such movements based on short-term monitoring and data collection.

SUMMARY

It is not our intention to belittle any of the biologists or RRT programs reviewed in this paper. We recognize that decision-making in conservation biology often is made by non-scientists or under crisis circumstances. Nonetheless, our review casts doubt on the effectiveness of RRT programs as a conservation strategy, at least for most species of amphibians and reptiles. Although RRT programs may work under certain circumstances, they should not be used unless all parties involved are prepared to make the necessary commitment for collecting baseline data, releasing animals under appropriate circumstances, providing for follow-up studies at periodic intervals, and publishing the methodology and results of the program regardless of whether the outcome is positive or negative. If such commitments cannot be made, other conservation strategies should be considered.

Acknowledgments.—We thank J. Diemer, R. Lohoefener, R. Martin, P. Moler, H. Quinn, R. Paine, R. Reynolds, H. Snell, I. J. Stout, S. Tonge, and D. Wood for information related to relocation activities. L. Close, D. Cundall, D. Formanowicz, Jr., R. Franz, R. Jaeger, and J. P. Ross provided thoughtful comments on the manuscript.

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Accepted: 3 December 1990
Associate Editor: David Cundall

Herpetologica, 47(3), 1991, 350–357

RELOCATIONS, REPATRIATIONS, AND TRANSLOCATIONS OF AMPHIBIANS AND REPTILES: TAKING A BROADER VIEW

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THE review of "relocation, repatriation and translocation" (RRT's) of amphibians and reptiles by Dodd and Seigel (1991) provides a summary of the literature on the use of these techniques for conservation purposes. Their recommendations are generally sound, and apply not only to these conservation practices, but equally well to any of the myriad possible techniques used to help insure the preservation of a species. However, I believe that the evidence they use for support is weak, that their dissatisfaction with past efforts is only partially justified, and thus their conclusions extreme. Basically, the question that they attempt to answer is: given that conservation dollars are always limited, are RRT's cost effective and appropriate procedures for amphibian and reptile conservation programs? They find that these techniques have been successful in only a few cases, and thus they propose a rigid set of criteria to be addressed before any future attempts are begun. My comments on their work focus on two main points: whether amphibians and reptiles are generally poor candidates for RRT's, and how success should be determined.

REPTILES AND AMPHIBIANS AS RRT CANDIDATES

As Griffith et al. (1989) did for a much larger number of studies of birds and mammals, Dodd and Seigel reviewed RRT programs for 25 species of amphibians and reptiles and found that of the 11 projects that could be defined as successful or unsuccessful by their standards, five (45%) were successful. This is slightly higher than the success rate reported for 198 RRT's reviewed by Griffith et al. Even so, the use of this type of analysis is exceedingly crude, because it assumes that snakes, lizards, turtles, crocodilians, salamanders, and anurans have comparable potential for successful RRT. Certainly there is wide variation within each order as well as between them, and anyone considering an

EXHIBIT LIST

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California Energy Resources Conservation and Development Commission

In the Matter of:

APPLICATION FOR CERTIFICATION
FOR THE IVANPAH SOLAR
ELECTRIC
GENERATING SYSTEM

DOCKET NO. 07-AFC-5

DECLARATION OF SERVICE

I, Lisa T. Belenky, declare that on December 17, 2009, I served and filed copies of the attached ***OPENING TESTIMONY FOR TOPICS TO BE HEARD IN JANUARY, 2010, EXHIBIT LIST, EXHIBITS, AND PROOF OF SERVICE INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY*** dated December 17, 2009. The original document, filed with the Docket Unit, is accompanied by a copy of the most recent Proof of Service list, located on the web page for this project at: [www.energy.ca.gov/sitingcases/ivanpah]. The document has been sent to the other parties in this proceeding (as shown on the Proof of Service list) and to the Commission's Docket Unit, in the following manner:

(Check all that Apply)
FOR SERVICE TO ALL OTHER PARTIES:

__X__ sent electronically to all email addresses on the Proof of Service list as listed below;
____ by personal delivery or by depositing in the United States mail at with first-class postage thereon fully prepaid and addressed as provided on the Proof of Service list above to those addresses NOT marked "email preferred."
AND

FOR FILING WITH THE ENERGY COMMISSION:
__X__ sending two paper copies and one electronic copy, mailed and emailed respectively, to the address below (preferred method);
OR
_____ depositing in the mail an original and 12 paper copies, as follows:

CALIFORNIA ENERGY COMMISSION
Attn: Docket No. 07 AFC 5
1516 Ninth Street, MS-4
Sacramento, CA 95814-5512
docket@energy.state.ca.us

I declare under penalty of perjury that the foregoing is true and correct.

Lisa T. Belenky

Lisa T. Belenky

Sent via email to: sdeyoung@brightsourceenergy.com; tstewart@brightsourceenergy.com; jcarrier@ch2m.com; jdh@eslawfirm.com; e-recipient@caiso.com; tom_hurshman@blm.gov; Raymond_Lee@ca.blm.gov; dfgpalm@adelphia.net; tgulesserian@adamsbroadwell.com; mjconnor@westernwatersheds.org; gloria.smith@sierraclub.org; devorah.ancel@sierraclub.org; joanne.spalding@sierraclub.org; gssilliman@csupomona.edu; jbasofin@defenders.org; atomictoadranch@netzero.net; gsuba@cnps.org; thansen@cnps.org; granites@telis.org; bbrizzee@cc.sbcounty.gov; jbyron@energy.state.ca.us; jboyd@energy.state.ca.us; pkramer@energy.state.ca.us; jkessler@energy.state.ca.us; dratliff@energy.state.ca.us; publicadviser@energy.state.ca.us; docket@energy.state.ca.us

Two paper copies of all documents and an electronic copy of all exhibits on a disk were sent via FedEx Overnight to:
CALIFORNIA ENERGY COMMISSION
Attn: Docket No. 07-AFC-5
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Electronic Copies of all exhibits were sent on a disk via U.S. Mail to:

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