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DOCKET
08-AFC-13
DATE AUG 25 2010
RECD. AUG 25 2010

August 25, 2010

California Energy Commission
Attn: Docket Office, 08-AFC-13
1516 Ninth Street
Sacramento, CA 95814

Re: Calico Solar; Docket No. 08-AFC-13

Dear Docket Clerk:

Please process the enclosed **CALIFORNIA UNIONS FOR RELIABLE ENERGY'S EXHIBITS 454 - 460,** conform the copy of the enclosed letter, and return the copy in the envelope provided.

Thank you.

Sincerely,

/S/

Loulena A. Miles

LAM:bh
Enclosures

2309-100a

STATE OF CALIFORNIA

California Energy Commission

In the Matter of: The Application for Certification for the CALICO SOLAR PROJECT (Formerly SES Solar One)	Docket No. 08-AFC-13

CALIFORNIA UNIONS FOR RELIABLE ENERGY 3RD REVISED SEQUENTIAL EXHIBIT LIST FOR THE CALICO SOLAR PROJECT

August 24, 2010

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EXHIBIT NO.	DATE	TITLE	SUBJECT	SPONSOR
400	7/23/10	Opening Testimony of David Marcus on Behalf of California Unions for Reliable Energy on Transmission for the Calico Solar Project	Transmission	David Marcus
401	7/16/10	Marcus Declaration	Transmission	David Marcus
402		Marcus c.v.	Transmission	David Marcus
403	4/26/10	131 FERC 61,071, Docket ER10-796, order issued April 26, 2010	Transmission	David Marcus
405	7/29/10	Rebuttal Testimony of Boris Poff on Behalf of California Unions for Reliable Energy on Soil and Water for the Calico Solar Project	Soil/Water	Boris Poff
406		Poff c.v.	Soil/Water	Boris Poff
407		McFadden, Wells, Jercinovich, Department of Geology, Univ. of New Mexico, Influences of eolian and pedogenic processes on the origin and evolution of desert pavements	Soil/Water	Boris Poff
408		Seager, Ting, Held, Kushnir, et al., Model Projections of an Imminent Transition to a More Arid Climate in Southwestern North America	Soil/Water	Boris Poff
409		Okin, Murray, Schlesinger, Degradation of sandy arid shrubland environments: observations, process modeling, and management implications	Soil/Water	Boris Poff
410		Okin, Gillette, Herrick, Multi-scale controls on and consequences of Aeolian processes in landscape change in arid and semi-arid environments	Soil/Water	Boris Poff
411		Angel, Palecki, Hollinger, Storm Precipitation in the United States. Part II: Soil Erosion Characteristics	Soil/Water	Boris Poff
412		Anderson, Wells, Graham, Pedogenesis of Vesicular Horizons, Cima Volcanic Field, Mojave Desert, California	Soil/Water	Boris Poff
413	7/29/10	Rebuttal Testimony of Vernon C. Bleich on Biological for the Calico Solar Project	Biology	Vernon Bleich
414		Bleich c.v.	Biology	Vernon Bleich

415	1996	Bleich, Wejaisem. Ramey, Rechel: Metapopulation Theory and Mountain Sheep: Implications for Conservation	Biology	Vernon C. Bleich
416		Epps, Wehausen, Bleich, Torres, Brashares: Optimizing dispersal and corridor models using landscape genetics	Biology	Vernon C. Bleich
417		Wehausen: Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep	Biology	Vernon C. Bleich
418		Oehler, Bleich, Bowyer, Nicholson: Mountain Sheep and Mining: Implications for Conservation and Management	Biology	Vernon C. Bleich
419		Schwartz, Bleich, Holl: Genetics and the Conservation of Mountain Sheep	Biology	Vernon C. Bleich
420	1990	Belich, Wehausen, Holl: Desert-dwelling Mountain Sheep: Conservation Implications of a Naturally Fragmented Distribution	Biology	Vernon C. Bleich
421		Bleich, Bowyer, Wehausen: Sexual Segregation in Mountain Sheep: Resources or Predation?	Biology	Vernon C. Bleich
422		Epps, Wehausen, Palsoboll, McCullough: Using Genetic Tools to Track Desert Bighorn Sheep Colonizations	Biology	Vernon C. Bleich
423	2000	Torres, Mulchahy, Gonzales, Pauli, Andrew: Human Induced Migration and Homing Behavior of a Desert Bighorn Ram in the Whipple Mountains, California: Or Herman the Trailer Park Ram	Biology	Vernon C. Bleich
424	7/29/10	Rebuttal Testimony of Scott Cashen on Biology for the Calico Solar Project	Biology	Scott Cashen
425		Cashen c.v.	Biology	Scott Cashen
426		Belnap, Webb, Miller, et al.: Monitoring Ecosystem Quality and Function in Arid Settings of the Mojave Desert	Biology	Scott Cashen
427		California Partners in Flight and PRBO Conservation Science: The Desert Bird Conservation Plan, a Strategy for Protecting and Managing Desert Habitats and Associated Bids in the Mojave and Colorado Deserts	Biology	Scott Cashen
428		U.S. Department of the Interior, USGS: Threats to Desert Tortoise Populations: A Critical Review of the Literature	Biology	Scott Cashen
429		U.S. Department of the Interior, USGS: Modeling Habitat of the Desert Tortoise (Gopherus agassizii) in the Mojave and Parts of	Biology	Scott Cashen

		the Sonoran Deserts of California, Nevada, Utah and Arizona		
430		Pagel, Whittington, Allen: Interim Golden Eagle Inventory and Monitoring Protocols; and Other Recommendations	Biology	Scott Cashen
431		Marzluff, Knick, Vekasky, Schuek, Zarriello: Spatial Use and Habitat Selection of Golden Eagles in Southwestern Idaho	Biology	Scott Cashen
432		Survey Protocols Required for NEPA/ESA Compliance for BLM Special Status Plant Species	Biology	Scott Cashen
433		Okin, Murray, Schlesinger: Degradation of sandy arid shrubland environments: observations, process modeling, and management implications	Biology	Scott Cashen
434	March 2006	Record of Decision, West Mojave Plan, Amendment to the California Desert Conservation Area Plan	Biology	Scott Cashen
435	August 2008	U.S. Dept. of Interior: Effects of the International Boundary Pedestrian Fence in the Vicinity of Lukeville, Arizona, on Drainage Systems and Infrastructure, Organ Pipe Cactus National Monument, Arizon	Biology	Scott Cashen
436		U.S. Fish and Wildlife Service: Final Environmental Assessment, Proposal to permit Take as provided Under the Bald and Golden Eagle Protection Act	Biology	Scott Cashen
437		Project Overview Map	Transmission	David Marcus
438	10/21/09	Transmission Line Upgrades	Transmission	David Marcus
439	2008/2009	Annual Reports for the Fort Irwin Translocation Project	Biology	Scott Cashen
440		Bighorn Habitat Connectivity Map	Biology	Vernon Bleich
441	8/16/10	Rebuttal Testimony of David S. Whitley on Behalf of the California Unions for Reliable Energy on Cultural Resources for the Calico Solar Project (c.v. and declaration)	Cultural	David S. Whitley
442	2001	Desert Pavement and Buried Archaeological Feature in the Arid West: A Case Study from Southern Arizona	Cultural	David S. Whitley
443	8/17/10	Testimony of Scott Cashen on Behalf of California Unions for Reliable Energy on the Desert Tortoise Translocation Plan for the Calico Solar Project (and Declaration)	Biology	Scott Cashen
444	2/2008	Desert Tortoise Council Abstracts 33rd Annual Meeting and Symposium	Biology	Scott Cashen

445	2/2009	Desert Tortoise Council Abstracts 34th Annual Meeting and Symposium	Biology	Scott Cashen
446	2/2010	Desert Tortoise Council Abstracts 35th Annual Meeting and Symposium	Biology	Scott Cashen
447	4/2/09	US Dept. of the Army, Memorandum for Desert Tortoise Recovery Coordinator, re Fort Irwin FISS Depredation	Biology	Scott Cashen
448	7/29/05	T. Esque, K. Nussear, P. Medica, Desert Tortoise Translocation Plan for Fort Irwin's Land Expansion Program at the U.S. Army National Training Center (NTC) & Fort Irwin	Biology	Scott Cashen
449	5/1/09	T. Esque, K. Nussear, K. Drake, K. Berry, P. Medica, J.Heaton, Amendment to Desert Tortoise Translocation Plan for Fort Irwin's Land Expansion Program at the U.S. Army National Training Center (NTC) & Fort Irwin	Biology	Scott Cashen
450	Spring 2010	Calico Solar Desert Tortoise Translocation Plan Recipient Site Photograph; Photograph #4: Long Distance DWMA Translocation Area	Biology	Scott Cashen
451		K.H. Berry, Draft Decision for Short-Distance Translocation of Desert Tortoises	Biology	Scott Cashen
452		Single Factor ANOVA Model and Tests, Control Treatment	Biology	Scott Cashen
453		K. Berry, M. Christopher, Guidelines for the Field Evaluation of Desert Tortoise Health and Disease	Biology	Scott Cashen
454	8/25/10	Testimony of Scott Cashen on Desert Tortoise Impacts in Staff's Errata #2	Biology	Scott Cashen
455		K.E. Nussear, T.C. Esque, D.F. Haines, C.R. Tracy, Desert Tortoise Hibernation: Temperatures, Timing and Environment	Biology	Scott Cashen
456		C.H. Ernst, J.E. Lovich, Turtles of the United States and Canada	Biology	Scott Cashen
457		J.M. Germano, P.J. Bishop, Suitability of Amphibians and Reptiles for Translocation	Biology	Scott Cashen
458		J.S. Heaton, et al., Spatially explicit decision support for selecting translocation areas for Mojave desert tortoises	Biology	Scott Cashen
459	9/14/04	Redlands Institute Decision Support Team, Habitat Potential Knowledge Base (cover and pp. 30-32)	Biology	Scott Cashen
460		Adaptive Management Working Group, The U.S. Dept. of the	Biology	Scott Cashen

EXHIBIT 454

STATE OF CALIFORNIA
California Energy Commission

In the Matter of:

The Application for Certification
for the **CALICO SOLAR PROJECT**

Docket No. 08-AFC-13

TESTIMONY OF SCOTT CASHEN ON DESERT TORTOISE IMPACTS IN STAFF'S ERRATA #2

August 25, 2010

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This testimony responds to the Energy Commission Staff's Addendum (Second Errata) to the Supplemental Staff Assessment for the Calico Solar Project ("Project"), which Staff distributed to the service list the evening of August 17, 2010. Specifically, I address the deficiencies of the proposed translocation plan that will affect up to 897 desert tortoises.[1]

I. Actions Required to Implement the Translocation Plan

Staff's Addendum states that the Project will require a series of actions to implement the proposed translocation plan.[2] At this time, many, if not most, of the required steps have not been completed, and neither the Staff Addendum nor the Applicant's proposed translocation plan adequately addresses the criteria that will be used to implement the plan.

Staff identified a minimum of 10 actions that would be required to translocate desert tortoises off the Project site.[3] In the subsequent section I provide a brief summary of each action, and I discuss why the action cannot be deferred until after Project approval if the translocation effort is to have a reasonable possibility of success.

a. Identification of the proposed translocation and control sites.

1. TRANSLOCATION SITES

The Applicant has not identified suitable translocation sites for the desert tortoises that would be removed from the Project site. Staff has determined that one of the "short-distance" translocation sites identified by the Applicant (i.e., the northern linkage area) is unlikely to be a viable translocation site, and the other short-distance translocation site would allow a maximum of two translocated tortoises, and "thus all other tortoises detected on the project site would require long distance translocation."[4]

The Applicant has identified two *potentially suitable* long-distance translocation sites (i.e., Ord-Rodman DWMA 1 and DWMA 2). According to Staff's Addendum, "information provided by the USFWS suggests that approximately 90 tortoises could be translocated to the Ord-Rodman Mountains DWMA. However, this estimate may be revised based on the results of the fall 2010 surveys."[5] The Addendum does not provide any rationale to support the statement that approximately 90 tortoises could be translocated to the Ord-Rodman Mountains DWMA. Furthermore, it is unclear whether Staff's estimate of 90 tortoises is being applied to the entire Ord-Rodman Mountains DWMA, or just to the Applicant's proposed recipient areas in the DWMA. The Addendum does not explain the discrepancy between its estimate, and the Applicant's Translocation Plan, which concluded a total of 60 tortoises could be translocated to the

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[1] [2nd Errata]. 2010 Aug 17. Energy Commission Staff's Second Errata to the Supplemental Staff Assessment for the Calico Solar Project (08-AFC-13).
[2] 2nd Errata, p. 9.
[3] *Id.*
[4] 2nd Errata, p. 11.
[5] 2nd Errata, p. 12.

Ord-Rodman DWMA recipient areas.[6] ***The Applicant's Translocation Plan provides inconsistent information, but states tortoise density in the recipient areas cannot exceed six (page 2-4) or seven (page 2-18) tortoises per km^2. Staff's Addendum indicates tortoise density in the Applicant's proposed translocation areas may already exceed these levels (i.e., they were estimated to be 8.2 tortoises per square kilometer in 2007).***[7] No matter the scenario or the values that are applied, the Applicant has yet to identify enough sites that are even *potentially suitable* for all the tortoises it estimates will require translocation.[8]

During the 18 August 2010 evidentiary hearings, the Bureau of Land Management's (BLM) witness, Chris Otahal, testified that translocation areas within the Ord-Rodman DWMA could be expanded to incorporate more tortoises. It is unclear how this might be accomplished, given (a) much of the land surrounding the currently proposed translocation areas is privately-held or designated wilderness (the BLM does not permit translocation into wilderness areas); and (b) the acceptable survey window for desert tortoise is narrow, and the Applicant has not even been able to survey much of the currently proposed translocation areas.[9]

2. CONTROL SITE

According to Staff's Addendum, the purpose of the control area is "to provide information regarding tortoise populations in an unaffected area for comparison to information obtained at the translocation sites."[10] The "control" area identified by the Applicant is heavily *affected* by past grazing practices, and thus it is not appropriate for comparison with translocation sites (i.e., as a control).[11] Neither Staff nor the Applicant has provided information on how the control area would be applied to scientific study. Specifically, neither provides even the most basic information on experimental design, data collection procedures, or statistical analyses that would be conducted. These issues result in a proposed control area that *cannot* be used to compare information obtained from the Project site.

b. The evaluation of the habitat quality on the translocation and control sites.

Germano and Bishop (2009) reviewed the results of 91 amphibian and reptile translocation projects published between 1991 and 2006. Based on this review, they concluded "[i]f the release habitat is not of high quality, then the chances of a positive outcome are low even when all other factors are taken into consideration. Although we could not evaluate habitat quality in the publications we reviewed, poor or unsuitable habitat was one of the most often reported reasons for translocation failure."[12] A

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[6] Applicant's Desert Tortoise Translocation Plan, p. 2-18.

[7] 2nd Errata, p. 12.

[8] *See* Exhibit 443, Testimony of Scott Cashen, p. 9.

[9] *See* Applicant's Desert Tortoise Translocation Plan, Figure 6.

[10] 2nd Errata, p. 11.

[11] *See* Exhibit 443, Testimony of Scott Cashen, p. 15.

[12] Germano, J.M. and Bishop, P.J. (2008) Suitability of amphibians and reptiles for translocation. Conservation Biology 23:(1) 7-15.

thorough evaluation of habitat quality at the translocation and control sites is an absolutely essential component of the translocation plan that must be provided before Project approval.

The Applicant has done very little to evaluate habitat at the proposed translocation and control sites. The Translocation Plan provides a limited amount of qualitative information that, in my opinion, shows clear signs of observer bias. The Translocation Plan does not provide any information on the methods that were used to obtain the qualitative data that it provides. The Translocation Plan also lacks any standards or criteria for evaluating the habitat that would allow subsequent surveyors to replicate the results. The Applicant's desert tortoise field survey forms do not document habitat parameters, nor does it appear the field crew was instructed to record them. Neither the Applicant nor Staff has identified the quality of habitat at the control site; however, the Translocation Plan states grazing has minimized desert tortoise resources at the control site (suggesting it provides low quality habitat).[13]

Neither the Applicant nor Staff has identified a process for obtaining reliable information on habitat quality at the translocation and control sites. The lack of information provided by the Applicant, BLM, and Staff on habitat quality makes it impossible to evaluate the suitability of the proposed translocation and control sites.

c. <u>A determination of existing tortoise density and an assessment of the site's ability to accommodate additional tortoises above baseline conditions.</u>

The Applicant has not reported the current (i.e., 2010) densities of tortoises within the proposed translocation and control sites. Accurate density estimates are necessary to ensure translocation sites can support additional tortoises. ***Staff's Addendum lacks a mechanism for attaining current density estimates, or even information on how and when these estimates will be provided.*** Furthermore, Staff's Addendum provides no discussion of the actions that will be taken to assess the ability of translocation sites to accommodate additional tortoises. Information provided in Staff's Addendum suggests that there are very few (if any) locations in the Project region that are capable of accommodating additional tortoises.[14]

d. <u>Pre-construction fencing and clearance surveys of the project site.</u>

Desert tortoises typically begin hibernation in October or November, but some may enter hibernacula as early as late August.[15] Winter burrows are relatively deep, usually 2 to 4.5 m, but occasionally 6 to 10 m.[16] Once in their burrows, desert tortoises resist almost all attempts to remove them.[17] The Applicant proposes to begin clearing tortoises off the Project site in October 2010. Neither the Applicant, BLM, nor Staff has addressed how

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[13] Applicant's Desert Tortoise Translocation Plan, p. 2-4.
[14] 2nd Errata, p. 12.
[15] Ernst CH, JE Lovich. 2009. p. 547.
[16] Ernst CH, JE Lovich. 2009. p. 548.
[17] Ernst CH, JE Lovich. 2009. p. 550.

the Applicant will determine whether tortoises might have entered their winter hibernacula before (or during) the Applicant's clearance surveys.

During the 18 August 2010 evidentiary hearings, the USFWS's representative, Ashleigh Blackford, indicated tracking equipment on tortoises at the Desert Tortoise Natural Area could be used to determine when tortoises where entering their winter hibernacula. Timing of hibernation by desert tortoises differs among sites and years.[18] As a result, data from the Desert Tortoise Natural Area cannot necessarily be used to establish hibernation dates at the Project site.

e. The construction of holding pens for quarantined translocated tortoises prior to their release into host populations.

There are many potentially significant impacts associated with construction and operation of quarantine pens.[19] These include the impacts of the pens on sensitive biological resources, the need to have an animal husbandry plan developed by a qualified veterinarian and approved by the Desert Tortoise Recovery Office prior to use of the pens, and the methods used to minimize predation at and near the pen sites. Neither the Applicant's Translocation Plan nor Staff's Addendum has addressed these issues.

f. Pre-construction surveys of the proposed translocation sites.

Scientifically defensible surveys are necessary to develop a meaningful translocation plan, and as such, they cannot be deferred until after Project approval.

g. The placement of tracking units (GPS) on tortoises from the project site, translocation site, and control site.

The Applicant's Translocation Plan makes no reference to placing GPS units on tortoises. The Applicant has proposed gluing radio-transmitters on tortoises, but it has not discussed how it will keep transmitters from falling off (loss of transmitters has been a major problem in the Fort Irwin translocation study).

h. Disease testing for long distance translocated tortoises, host, and control sites.

When tortoises are translocated, their health status and overall condition at the time of translocation are likely to be factors influencing later well-being and survival.[20] The Applicant has not conducted any disease testing, and it only plans to conduct testing

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[18] Nussear KE, TC Esque, DF Haines, CR Tracy. 2007. Desert Tortoise Hibernation: Temperatures, Timing, and Environment. Copeia 2007(2): 378-386.

[19] *See* Exhibit 443, Testimony of Scott Cashen, p. 19.

[20] Berry KN, T Gowan, JS Mack. 2009. Health and Survival of 158 Tortoises Translocated from Ft. Irwin: Year 1 of the Health Research Program. [Abstract]. Thirty-fourth Annual Meeting and Symposium; 2009 Feb 20-22, Mesquite (NV). The Desert Tortoise Council. Available from: http://www.deserttortoise.org/symposia.html.

during the process of clearing tortoises off the Project site.[21] As a result, it will have no knowledge of whether the animals it is moving are sick or healthy. This increases the risks of contamination and mortality.

The Applicant has not identified the diseases for which testing will be conducted, or the specific methods that will be used to test diseases (e.g., blood draw location). However, the recent research has shown that there are several fundamental problems associated with the traditional approach of developing a list of diseases of concern, testing release candidates for those diseases, and making release decisions based on the test results.[22] The Applicant's Translocation Plan does not address these problems, or provide any other analysis related to disease screening. Without additional analysis, the Applicant will risk euthanizing perfectly healthy animals and the unintentional release of diseased individuals.[23] Neither the Applicant's Translocation Plan nor Staff's Addendum discuss how disease testing will be conducted to minimize errors, the anticipated reliability of the results, or the process for making decisions on the fate of animals based on the test results.

i. <u>Long term monitoring and reporting of control and translocated and host populations.</u>

The Applicant's Translocation Plan provides inconsistent information on the duration of monitoring after translocation.[24] During the 18 August 2010 evidentiary hearings, the BLM's witness, Chris Otahal, testified that the Applicant's proposed monitoring would provide "very good management direction"; is "designed like a science project more than a monitoring program"; and "it's very rigorous."[25] Mr. Otahal's statements lack scientific merit.

First, the Plan does not propose adequate long-term monitoring. Numerous publications have reported it can take 15–20 years before success of a translocation project can be reliably evaluated (e.g., Dodd and Seigel 1991; Nelson et al. 2002; Bell et al. 2004). Many researchers have advocated for better monitoring (Griffith et al. 1989; Dodd and Seigel 1991; Seddon 1999; Fischer and Lidenmayer 2000), and have concluded that it is vital that all organizations carrying out translocations commit to the long-term monitoring that is essential for these projects.[26] Through my review of numerous publications that discussed translocation, <u>none</u> suggested a five-year monitoring program was sufficient for evaluating the success of translocation, especially for projects involving desert tortoises.

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[21] Applicant's Desert Tortoise Translocation Plan, Table 4.

[22] Rideout BA. 2010. The Pitfalls of Using Test Results for Decision-Making in Conservation Programs [Abstract]. Thirty-fifth Annual Meeting and Symposium; 2010 Feb 25-28, Ontario (CA). The Desert Tortoise Council. Available from: http://www.deserttortoise.org/symposia.html.

[23] *Id.*

[24] Applicant's Translocation Plan page 1-4 states 5 years, whereas page 2-10 states 3 years.

[25] Testimony of Chris Otahal. 2010 Aug 18. p. 368.

[26] Germano, J.M. and Bishop, P.J. (2008) Suitability of amphibians and reptiles for translocation. Conservation Biology 23:(1) 7-15.

Second, the Applicant's proposed Translocation Plan has almost no rigor. Instead, it is plagued by a vague and inconsistent study plan, hastily derived information, and a complete lack of analysis. The Applicant's own consultant has repeatedly stated that the information used to develop the plan was obtained through a qualitative assessment.[27] Generally, a non-quantitative description limited in scope and depth of detail is considered an anecdote.[28] Anecdotes usually lack any formal documentation and are most often made by untrained, casual observers, but professionals often report anecdotal observations.[29] *Anecdotes are highly risky for basing management decisions because of their lack of rigor, repeatability, and objectivity.*[30]

Anecdotes need to be properly evaluated using sound scientific methodology.[31] They can often form the basis for more formal observations, hypothesis development, or experimentation.[32] Occasionally, there are attempts to legitimize anecdotes by compiling many into a single report and attempting a quantified or statistical treatment (*see, e.g.*, Section 2.1.2.1 of the Translocation Plan).[33] These are misguided attempts because the extreme weakness and subjectivity of the basic data limit the ability to conduct any meaningful analyses. The plural of anecdote is not data.[34] *The Applicant's Translocation Plan is based almost entirely on anecdotes—not data.*

People often make guesses about possibilities for which there are no hard data (e.g., *see* Section 2.6.3 of the Translocation Plan). When those guesses are based on clearly stated and well-founded assumptions, the guesses are called hypotheses and can help to direct future conceptual and experimental pursuits (Resnik 1991). When assumptions are weak or unstated, the guesses are speculations.[35] Speculations may be seductive; they often present a series of progressively dependent statements that have an internal logic of their own. The logic may appear compelling and is often bolstered by attempts to provide "proof" through analogies. Such argumentation often collapses when primary assumptions are nullified or when they are tested against real data, but too often the test is never made.[36] Although they may sometimes form the basis for hypotheses and experiments, *speculations are risky to base management decisions because there is*

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[27] Testimony of Theresa Miller. 2010 Aug 18. p. 334.

[28] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

[29] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

[30] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

[31] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

[32] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

[33] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

[34] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

[35] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

[36] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

essentially no way to evaluate them and their predictive value is low.[37]

Finally, Mr. Otahal's attempt to suggest the Applicant's translocation program is rigorous and has resemblance to the scientific method is completely unsupported. Fundamental concepts of wildlife research and study design are summarized in Garton et al. (2005).[38] The authors reported that quality scientific investigations—ones that produce objective, relevant information—are dependent on carefully designed experiments, comparisons, and models. In short, they require application of the scientific method. The Applicant's Translocation Plan does not rely upon the scientific method in the development of the research plan and has not applied the scientific method in the plan's implementation to date.

j. The implementation of remedial actions should excessive predation or mortality be observed.

Neither the Applicant, BLM, nor Staff has established a standard or criterion that would indicate "excessive predation or mortality." Furthermore, neither the Translocation Plan nor Staff's Addendum discuss the remedial actions that might be taken if excessive predation or mortality occurs, nor do they provide the triggers for taking said actions.

During the 18 August 2010 evidentiary hearings, the BLM's witness, Chris Otahal, testified that success criteria are outlined in the Applicant's Translocation Plan.[39] Mr. Otahal's statement is incorrect. The Translocation Plan outlines the variables that should be measured to evaluate success (e.g., survivorship, growth rates, movement), but it does not provide any success criteria.[40]

Recent guidance issued by the U.S. Fish and Wildlife Service states: "[e]xplicit triggers for implementation of adaptive management will be project specific and developed through coordination with USFWS and State wildlife agencies, as appropriate."[41] Furthermore, CEQA requires that each public agency adopt objectives, criteria, and specific procedures to administer its responsibilities under the Act and the CEQA Guidelines (Section 21082). ***The environmental impacts of the Translocation Plan cannot be evaluated until specific success criteria and triggers for adaptive management have been established and the likelihood that proposed management action would be successful have been assessed.***

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[37] Boarman WI. 2002. Threats to Desert Tortoise Populations: A Critical Review of the Literature. U.S. Geological Survey, Western Ecological Research Center. Sacramento (CA): 86 p.

[38] Garton EO, JT Ratti, JH Giudice. 2005. Research and Experimental Design. Pages 185-196 in CE Braun, editor. Techniques for Wildlife Investigations and Management. The Wildlife Society, Bethesda (MD).

[39] Testimony of Chris Otahal. 2010 Aug 18. p. 370.

[40] *See* Translocation Plan, p. 2-24.

[41] USFWS. 2010 Aug. Translocation of Desert Tortoises (Mojave Population) From Project Sites: Plan Development Guidance.

II. Adaptive Management

During the 18 August 2010 evidentiary hearings, various parties discussed the need to identify sufficient desert tortoise translocation sites. Dr. Larry LaPré from the BLM stated "the Bureau of Land Management is the owner and manager of the recipient sites, and if we're going to have a major change or expansion to the location of those or the area of those [translocation sites], I don't think we should do that lightly."[42] The BLM's witness, Chris Odahal, responded by stating:

> "the idea was to address that basically a little bit further down the road as we start moving these tortoises, because the numbers are very rough guesstimates of what the numbers of animals are out there. And until we actually start moving them, we're not going to know exactly how many animals we're going to be moving and how much additional area we will need. And if you do read the translocation plan this is one of those adaptive management type of scenarios that is anticipated, because we fully understood that we may run out of receptor area during the translocation. Right now, we had some data earlier than we were anticipate to go see that, okay, we may be running out of room on the areas that we have already identified and that we have already done our surveys, but again, we were fully intending in adaptive management standpoint to be expanding those areas if need be."[43]

Mr. Otahal's testimony completely misconstrues the meaning of adaptive management. The U.S. Department of the Interior, which encompasses the Bureau of Land Management, defines adaptive management as "*a systematic approach for improving resource management by learning from management outcomes*."[44] In discussing adaptive management, Morrison (2002) added:

1. "The concept of adaptive management or adaptive resource management is centered primarily on monitoring the effects of land-use activities on key resources and then using the monitoring results as a basis for modifying those activities to achieve the project's goals (Walters 1986; Lancia et al. 1996)."
2. "Adaptive management is not a trial-and-error approach."
3. "Attempting to fix a problem after implementation is quite different from developing an action plan prior to the start of a project."
4. "Regardless of the specific approach, adaptive management offers a structure whereby clear goals are established and then monitored—and specific actions for responding to deviations are planned at the *outset* of the project."[45]

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[42] Testimony of Larry LaPré. 2010 Aug 18. p. 278.

[43] Testimony of Chris Otahal. 2010 Aug 18. p. 279.

[44] Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2009. Adaptive Management: The U.S. Department of the Interior Technical Guide. Adaptive Management Working Group, U.S. Department of the Interior, Washington, DC.

[45] Morrison ML. 2002. Wildlife Restoration: Techniques for Habitat Analysis and Animal Monitoring. Island Press: Washington (DC).

The Applicant's and BLM's failure to identify a sufficient number of translocation sites is not adaptive management; it is poor planning that is likely to result in unnecessary mortality to desert tortoises. The Applicant, BLM, and Staff have developed an estimate of the number of tortoises requiring translocation—and a 95% confidence interval for the estimate. By definition, the confidence interval reflects the reliability of the estimate.[46] If it was generated properly, it provides a precise estimate of the number of tortoises that will require translocation, not a "very rough guesstimate" as suggested by Mr. Otahal. Staff can and should rely on the estimate from the 95% confidence interval and develop adequate translocation sites for this estimated number of tortoises.

III. Conclusion

Research on desert tortoise translocation has identified the dangers associated with introducing new tortoises to a population; the importance of selecting adequate receptor sites; and the need to carefully consider the methods used to implement translocation.[47] Based on the information provided by the Applicant, BLM and Staff, it is impossible to determine either the efficacy of the proposed translocation plan, or the impact implementation of the plan will have on the receptor sites. Although Staff's Addendum lists several actions required to implement the translocation plan, it lacks a funding mechanism to ensure the tasks are completed and that Staff's intent is satisfied. The tasks identified by Staff will require considerable surveying and analysis. Consequently, one cannot reliably assume they will occur, and that deferred analysis will identify adequate receptor sites. Finally, neither the Staff Addendum nor the Applicant's proposed Translocation Plan contains the standards and criteria necessary to evaluate the adequacy of translocation lands, or the translocation program as a whole. In my professional opinion, neither Staff's Addendum nor the Applicant's Translocation Plan provides the framework for an adequate translocation effort and will likely result in the unnecessary mortality of desert tortoises.

Further, there is no indication that sufficient translocation lands are available for the estimated number of tortoises on the Project site. Additional sites must be identified prior to project approval and analyzed in accordance with CEQA. Each of the potentially significant, direct and indirect impacts to tortoises and other biological resources at these translocation sites must be included in this analysis. The Project has the potential to eliminate an entire generation (e.g., through mortality to a high number of juveniles), or local population (e.g., through spread of disease) of tortoises. These impacts must be fully analyzed in a revised CEQA document and circulated for public review. A fully realized translocation plan for the entire Project must be vetted and in place before a single tortoise is moved.

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[46] Lancia RA, WL Kendall, KH Pollock, JD Nichols. 2005. Estimating the Number of Animals in Wildlife Populations. Pages 106-153 in CE Braun, editor. Techniques for Wildlife Investigations and Management. The Wildlife Society, Bethesda (MD).

[47] Redlands Institute Decision Support Team. 2004. Desert Tortoise habitat potential knowledge base. Redlands Institute, Redlands, CA. Appendix B, p 30-32.

Declaration of Scott Cashen
Calico Solar Project

Docket 08-AFC-13

I, Scott Cashen, declare as follows:

1) I am an independent biological resources consultant. I have been operating my own consulting business for the past three years. Prior to starting my own business I was the Senior Biologist for TSS Consultants.

2) I hold a Master's degree in Wildlife and Fisheries Science. My relevant professional qualifications and experience are set forth in the attached testimony and are incorporated herein by reference.

3) I prepared the testimony attached hereto and incorporated herein by reference, relating to the biological resource impacts of the Calico Solar Project.

4) I prepared the rebuttal testimony and maps attached hereto and incorporated herein by reference relating to the distribution of solar energy generation infrastructure in San Bernardino County.

5) It is my professional opinion that the attached rebuttal 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: 8-25-10

Signed:

At: Walnut Creek, CA

EXHIBIT 455

Copeia, 2007(2), pp. 378–386

Desert Tortoise Hibernation: Temperatures, Timing, and Environment

KENNETH E. NUSSEAR, TODD C. ESQUE, DUSTIN F. HAINES, AND C. RICHARD TRACY

This research examined the onset, duration, and termination of hibernation in Desert Tortoises (*Gopherus agassizii*) over several years at multiple sites in the northeastern part of their geographic range, and recorded the temperatures experienced by tortoises during winter hibernation. The timing of hibernation by Desert Tortoises differed among sites and years. Environmental cues acting over the short-term did not appear to influence the timing of the hibernation period. Different individual tortoises entered hibernation over as many as 44 days in the fall and emerged from hibernation over as many as 49 days in the spring. This range of variation in the timing of hibernation indicates a weak influence at best of exogenous cues hypothesized to trigger and terminate hibernation. There do appear to be regional trends in hibernation behavior as hibernation tended to begin earlier and continue longer at sites that were higher in elevation and generally cooler. The emergence date was generally more similar among study sites than the date of onset. While the climate and the subsequent timing of hibernation differed among sites, the average temperatures experienced by tortoises while hibernating differed by only about five degrees from the coldest site to the warmest site.

DESERT Tortoises (*Gopherus agassizii*) are distributed in desert and subtropical regions of the southwestern United States and northern Mexico (Germano et al., 1994). The northern extent of this distribution is a temperate zone where some environmental temperatures in winter can be inhospitable or even lethal to Desert Tortoises. Tortoises avoid cold temperatures in the winter by using underground cover sites (hibernacula), which generally consist of burrows (excavated in soil) or dens (natural rocky caves; Burge, 1977; Bulova, 1994). Hibernacula generally have higher temperatures than the open environment during the winter and provide substantial buffering from the daily temperature fluctuations present in the environment. Thus, hibernacula provide tortoises with protection from potentially lethal temperatures in winter.

Research on the timing and temperature of reptile hibernation has focused on snakes (Viitanen, 1967; Sexton and Hunt, 1980; Blouin-Demers et al., 2000), lizards (Garrick, 1972; Etheridge et al., 1983; Wone and Beauchamp, 2003), and turtles (Grobman, 1990; Litzgus et al., 1999; Plummer, 2004), but few studies have focused on tortoises (Vaughan, 1984; Bailey et al., 1995; Rautenstrauch et al., 1998). Understanding the timing of hibernation of Desert Tortoises could have important management implications for this sensitive species (Rautenstrauch et al., 1998).

In the northeastern extent of their range, tortoises may hibernate for up to six continuous months (Woodbury and Hardy, 1948; Bury et al., 1994). Little is known about the mechanisms cuing the onset and termination of hibernation behavior or the amount of variation that should be expected to occur within the timing of this behavior. Potential cues for hibernation onset include reduced day length/photoperiod, cooler environmental temperatures, reduced forage availability, and timing of precipitation events (Gregory, 1982). Hibernation is thought to be advantageous by facilitating a reduction of metabolism during a time of the year with few resources. Tortoises, like other ectotherms, may be able to conserve energy by hibernating, as there is a concomitant reduction of metabolism with decreased body temperatures (Bennett and Dawson, 1976; Gregory, 1982). Tortoises may further reduce their metabolism by inverse acclimation or other mechanisms of metabolic depression (Gregory, 1982). This could allow tortoises to conserve energy during seasons with essentially no food resources. Alternatively, hibernation may be induced by endogenous cues. There is relatively little literature on endogenous mechanisms cuing hibernation, but observations of behavior such as declining appetite and shelter-seeking behavior under differential exposure to external cues suggest that the hibernation of some reptiles may be influenced by endogenous rhythms (Gregory, 1982). Although intriguing, this hypothesis is beyond the scope of the work we describe here.

In this study we examine correlations between the onset, duration, and termination of hibernation in Desert Tortoises in relation to potential exogenous cues over several years at multiple sites in the northeastern portion of their range. We report the temperatures experienced by Desert Tortoises and their associated behavior during winter hibernation.

MATERIALS AND METHODS

Study sites.—We studied hibernation in Desert Tortoises at four sites in the northeastern Mojave Desert. The sites were located in the Mojave Desert scrub biome (Turner, 1982). The City Creek Site was located in Washington County north of St. George, Utah (37°9′00″N, 113°35′24″W), and ranged in elevation from 975 m to 1067 m, with highly variable topography: flat areas, dry washes up to 2 m deep, dunes, rocky cliffs and steep hills. The predominant substrate was red Navajo sandstone interspersed with ancient lava flows, sand dunes, and cryptobiotic soils (Esque, 1994). The Littlefield Site was located in Mohave County north of Littlefield, Arizona (36°55′48″N, 113°54′36″W), and ranged in elevation from 576 m to 622 m. The topography was generally flat (2–5% slope), with numerous dry washes up to 3 m deep (Esque, 1994). The substrate was shallow sandy/gravelly loam up to 0.6 m deep with an underlying calcium carbonate (caliche) hardpan layer. The Lake Mead site was located in Clark County, Nevada (36°29′24″N, 114°21′00″W). The site was at the northern end (Overton arm) of the Lake Mead National Recreation Area, near Overton, Nevada. The site elevation ranged from lake level (approximately 325 m) to 597 m and consisted of the top and steep cliff sides of a mesa bordered on three sides by water. The soil consisted of coarse alluvium consolidated by calcium carbonate, interspersed with patches of windblown sand. The Bird Spring Valley site was also in Clark County, Nevada (BSV 35°58′12″N, 115°20′24″W). The valley was an extensive bajada ranging from 900 m to 1300 m in elevation and was of relatively even terrain with shallow arroyos lined by occasional caliche caves. The substrate was sandy/gravelly loam up to 0.75 m deep with an underlying hardpan layer composed of caliche. Mountainous peaks bordered Bird Spring Valley to both the east and west.

Tortoise body temperatures.—We used miniature data loggers (Stowaway #STEB16, Onset Computer Corporation, Pocasset, MA) to record body temperatures during hibernation of wild Desert Tortoises at the City Creek and Littlefield sites. Data loggers were 26.5 g and came encased in a plastic rectangular housing (4.6 × 4.8 × 1.5 cm). They were calibrated in water baths at temperatures over a range of 0 to 45 C before and after use in the field. Data loggers were programmed to record temperatures once per hour. For protection from the environment, they were wrapped in a layer of paper and covered with a layer of duct tape followed by a coating of epoxy (which served as weather-proofing). Each data logger was attached with 5-minute epoxy gel to a location on the anterior half of the carapace to avoid potential interference during copulation. Data loggers were placed on animals prior to the expected onset of hibernation and were removed within several weeks after emergence from hibernation. Temperatures recorded by the data loggers at these two sites were the temperatures measured inside the plastic casing of the data loggers, not body temperatures of the tortoises. Nevertheless, the data from the loggers could be used to discern the timing of hibernation (see below), and temperatures of the loggers were likely similar to body temperatures while the animals were in hibernacula (Gregory, 1982).

Body temperatures of tortoises at the Lake Mead and Bird Spring Valley sites were measured using StowAway™ TidbiT™ temperature data loggers (Onset Computer Corporation, Pocasset, MA), customized by Onset from their standard design (TBICU108; −20 C to +70 C). These were 25 mm in diameter, 14 mm thick, and weighed approximately 15 g. They had a weather-resistant thermistor at the end of a 150-mm wire, which was affixed using fast-setting glue and silicone between the tail and the carapace of the tortoise (Nussear et al., 2002). This location has been shown to approximate cloacal temperatures of Desert Tortoises (Nussear et al., 2002).

Timing of hibernation.—We recorded data on hibernating tortoises over the course of four winters from 1995 to 1998 at the City Creek and Littlefield sites, and for one winter (1998–1999) at the Lake Mead and Bird Spring Valley sites. At City Creek we studied nine animals during the winter of 1995, ten animals in the winter of 1996 and 1997, and six animals in the winter of 1998. At Littlefield we studied four animals in the winter of 1995, six animals in the winter of 1996, 11 animals in the winter of 1997, and five animals in the winter of 1998. During the winter of 1998 we added tortoises at the Bird Spring Valley and Lake Mead sites to the study. We studied seven animals at Bird Spring Valley and nine animals at Lake Mead.

Onset, duration, and termination of hibernation were interpreted from graphs of hourly body temperatures by locating the date when the amplitude of the daily fluctuations became noticeably reduced or increased. The accuracy of this interpretation was verified by weekly observations of the tortoises in the field. Patterns of temperatures of the data loggers at the City Creek and Littlefield study sites were clearly different when the tortoises were in and out of burrows. We defined onset of hibernation as the Julian date after which a tortoise did not emerge from its hibernaculum for at least 14 days. Likewise, the termination of hibernation was defined as the Julian date when a tortoise emerged from the hibernaculum, without returning for at least 14 days. The ''14-day'' criterion allowed for a consistent quantification of the onset and termination dates for animals that had false onsets or brief emergences during hibernation. These criteria are similar to those used by Bailey et al. (1995). Some data loggers became overloaded with data and stopped recording temperatures before the tortoise emerged from hibernation. This was due to logistical constraints encountered when changing the recording intervals of the dataloggers from active season intervals (15 min) to winter intervals (60 min). Thus, for some individuals, duration and termination of hibernation could not be calculated, although hibernation start dates were recorded.

We defined ''average hibernation temperature'' as the mean temperature of all measurements while an animal was hibernating. The ''mid-hibernation temperature'' was defined as the average temperature during the week of the winter solstice (i.e., week 51), and the ''minimum temperature'' as the lowest temperature experienced by the animal at any time during the hibernation period.

We compared Julian dates of onset and termination, duration of hibernation, and the mean, minimum, and mid-hibernation temperatures using ANOVA with site and year as factors. Repeated measurements of animals were accounted for by using a nested, split-plot design with tortoises nested within site treated as a random effect in order to allow for independent contrast analyses of the interaction term. Multiple comparisons to discern differences within significant effects were conducted using Tukey's-HSD.

Thermal buffering categories.—Cover sites were classified by the degree of thermal buffering that they provided as interpreted by the daily and biweekly patterns in body temperature. The greatest buffering was represented by a pattern in which the body temperature was nearly constant, with a difference of less than 1 C between the daily maximum and daily minimum temperatures for each tortoise. In addition, the average of the differences of absolute minimum and maximum temperatures for all successive 14-day periods throughout the hibernation period was <1.5 C. Less buffering resulted in body temperatures that still retained differences of daily maximum and minimum temperatures of less than 1 C. However, the body temperatures were influenced by local weather patterns when examined over longer time periods. In this category the average of the differences in the absolute maximum and absolute minimum temperatures for successive 14-day periods was greater than 1.5 C. The least buffering resulted in body temperatures that fluctuated greatly on a daily basis where the difference between the maximum and minimum daily temperature was more than 1 C. Analyses of the degree of thermal buffering of hibernacula were conducted for Littlefield and City Creek for the four years studied and among all four sites for the winter of 1998–1999 using Fisher's exact tests for contingency tables.

Meteorological data.—Climate data for the study sites were obtained from (1) City Creek: St. George, Utah, weather station 4 km south of the City Creek site, (2) Littlefield: Littlefield 1 NE station 10 km north of the Littlefield site, (3) Lake Mead: Overton station 1 km northwest of the site, and (4) Bird Spring Valley: Red Rock Canyon weather station 4 km northeast of the site (National Oceanic and Atmospheric Administration, 1998). Soil temperatures during the winter of 1998 at Bird Spring Valley were measured at a central location at the site using a CR-10 weather station (Campbell Scientific, Logan, UT) and type K thermocouples (Omega Engineering, Stamford, CT) at the surface and buried 70 cm below the surface, just above the caliche layer. Air temperature data for all four years were not available for the Littlefield site. We conducted regression analyses of the average air temperatures for the months of October and March on the average onset and termination dates of hibernation for each site to examine correlates of regional climate and hibernation patterns.

RESULTS

City Creek and Littlefield.—There was no overall difference for the average date of hibernation onset between tortoises at City Creek and Littlefield ($F_{1,32} = 3.26$; $P = 0.08$; Fig. 1). There were differences in the onset date among years. The average date of onset in the fall of 1995 (3 Nov. ± 1 SD = 12 d) was approximately nine days later than the average date of onset in the fall of 1996 (25 Oct. ± 1 SD = 8 d; Tukey's HSD

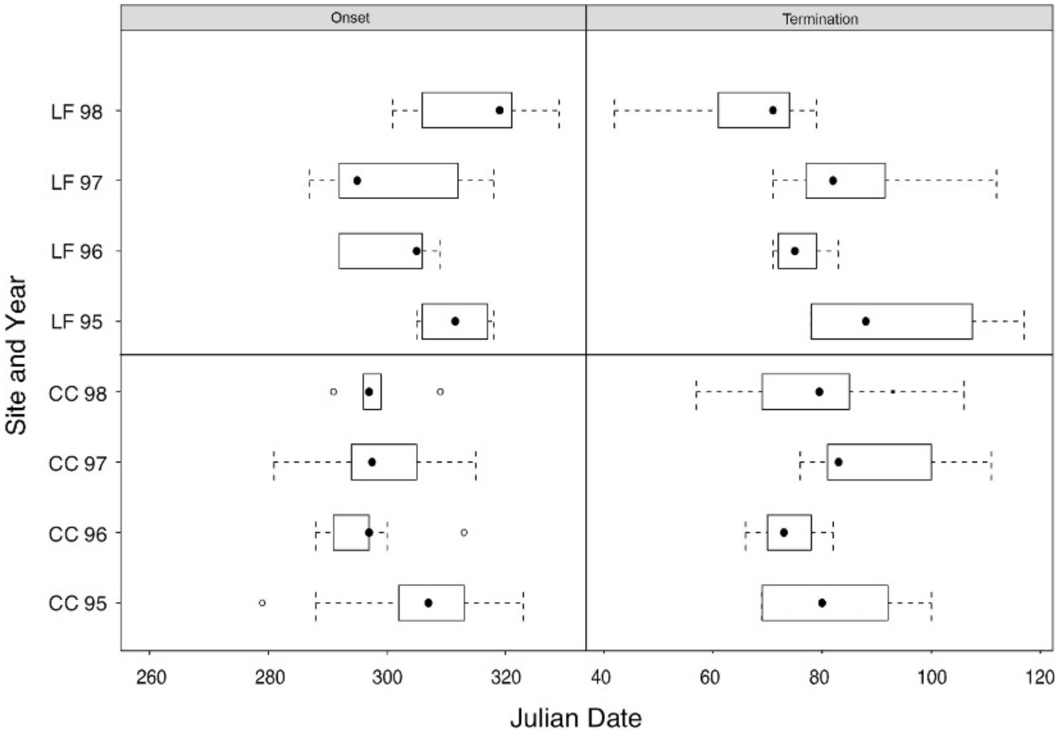

Fig. 1. Onset, duration, and termination of hibernation at the City Creek and Littlefield sites for the four winters from 1995 through 1998. The four winters at Littlefield are in the top half of the figure; City Creek is given in the bottom half. Years are sorted from bottom to top in each panel and listed as the year in which each hibernation period began. The distance between the onset and termination dates is the duration of hibernation. The median onset and termination dates for each site are shown as filled circles. The box surrounding the filled circle depicts the 25th and 75th quartile. The range of values for each measure is given by the dotted lines (''whiskers'') outside of each box, and possible outliers are given by the open circles outside the box.

$Q = 2.72$; $P < 0.05$). The onset dates for all other years were statistically indistinguishable from one another. There were no site-by-year interactions for onset date ($F_{3,29} = 0.65$; $P = 0.59$).

Tortoises at the City Creek and Littlefield sites spent a similar number of days in hibernation, ranging from 106 to 182 days ($F_{1,23} = 2.22$; $P = 0.15$; Fig. 1). The duration of hibernation varied among years coincident with a twenty-one day difference in duration of hibernation in the winters of 1997–1998 and 1998–1999 (154 ± 1 SD = 21 vs. 133 ± 1 SD = 21 days, respectively; Tukey's HSD $Q = 2.73$; $P < 0.05$). The durations of hibernation for all other years were statistically indistinguishable from one another. There was a significant year-by-site interaction due to animals at Littlefield during the 1998–1999 season having a shorter duration (134 ± 1 SD = 40 days) than the City Creek or Littlefield animals in the 1997–1998 season (154 ± 1 SD = 17 and 155 ± 1 SD = 25 days respectively; Tukey's HSD $Q = 3.27$; $P < 0.05$; Fig. 1).

The ending date for hibernation in the spring did not differ between the two sites and ranged between 11 February to 27 April ($F_{1,23} = 0.07$; $P = 0.79$; Fig. 1). There were significant differences in the termination date among years. In particular, the termination of hibernation (averaged for both sites) was earlier in the spring of 1996–1997 (15 March ± 1 SD = 5 d), and in the spring of 1998–1999 (14 March ± 1 SD = 17 d) than in the spring of 1995–1996 (25 March ± 1 SD = 15 d) or 1997–1998 (1 April ± 1 SD = 19 d; Tukey's HSD $Q = 2.72$; $P < 0.05$). There was a marginally non-significant site-by-year interaction for termination date ($F_{3,29} = 2.76$; $P = 0.06$).

There were no differences found in the average hibernation body temperature between City Creek and Littlefield ($F_{1,23} = 1.52$; $P = 0.23$; Table 1), but there were differences among years ($F_{3,30} = 6.86$; $P = 0.0012$). The average hibernation body temperature of tortoises during the winter of 1996–1997 (12 C) was approximately two degrees cooler than either 1997–1998 (14 C)

TABLE 1. TORTOISE BODY TEMPERATURES DURING HIBERNATION FOR THE WINTERS OF 1995–1999 AT CITY CREEK (CC), LITTLEFIELD (LF), BIRD SPRING VALLEY (BSV), AND LAKE MEAD (LM).

Year/site	Mean temperature (°C) ± 1 SD	Minimum temperature (°C) ± 1 SD	Mid-hibernation average (°C) ± 1 SD
1995			
CC	12.2 ± 1.1	8.2 ± 2.3	10.3 ± 2.4
LF	16.0 ± 3.8	9.7 ± 6.0	16.3 ± 6.4
1996			
CC	11.4 ± 1.5	6.5 ± 2.4	10.2 ± 1.4
LF	12.1 ± 1.5	7.9 ± 3.4	11.3 ± 2.2
1997			
CC	13.4 ± 2.0	9.3 ± 2.2	10.7 ± 3.2
LF	14.9 ± 4.4	10.1 ± 5.4	12.7 ± 6.3
1998			
BSV	14.7 ± 3.3	9.4 ± 4.6	10.0 ± 3.5
CC	11.9 ± 3.1	8.1 ± 3.4	8.9 ± 3.9
LF	12.8 ± 4.9	8.3 ± 6.6	11.4 ± 6.1
LM	15.2 ± 1.9	9.9 ± 4.29	12.7 ± 2.5

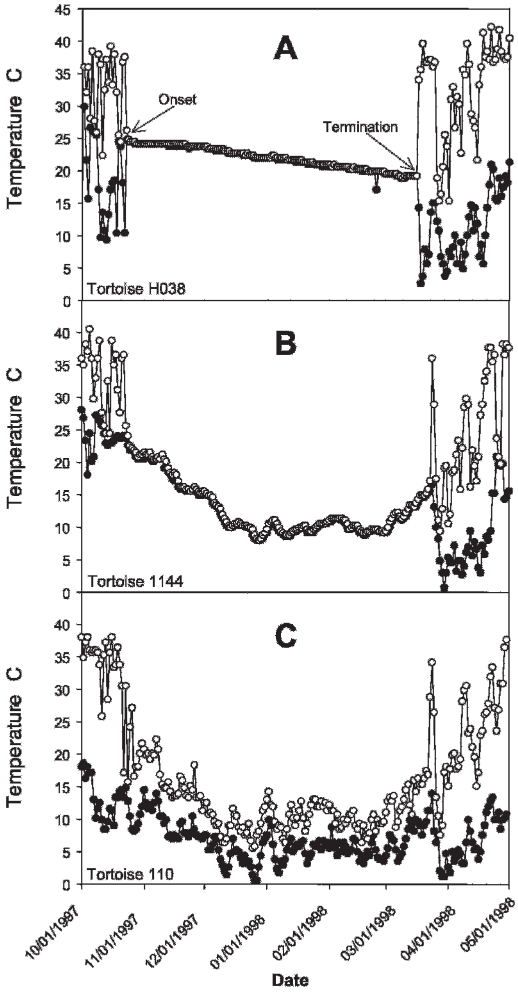

Fig. 2. Three examples of tortoise body temperatures prior to, during, and following hibernation. Data are presented as the daily minimum (filled circles) and maximum (unfilled circles) temperatures (C). Panel A is an example of a high buffering in the body temperature pattern. Panel B demonstrates a medium level of temperature buffering during hibernation. Panel C is an example of a low temperature buffering.

or 1995–1996 (14.2 C; Tukey's HSD $Q = 2.72$; $P < 0.05$). There were no significant site-by-year interactions ($F_{3,30} = 1.33$; $P = 0.29$). The mid-hibernation temperature did not differ between the two sites ($F_{1,23} = 1.89$; $P = 0.18$). There were differences among years in that the animals' temperatures during the 51st week of 1998 (9.88 C) were significantly cooler than during the same week in 1995 (13.13 C). The average minimum temperature experienced did not significantly differ for either site ($F_{1,23} = 0.17$; $P = 0.68$) or year ($F_{3,30} = 2.79$; $P = 0.058$).

We categorized the degree to which tortoises were insulated from environmental variation in temperature into three distinct patterns (Fig. 2). The numbers of animals that used hibernacula with these patterns differed among sites during three of the four winters of our study (Table 2). In those three years, tortoises at City Creek were mostly found in hibernacula with medium buffering (Fig. 2B), whereas tortoises at Littlefield occupied either no hibernacula in that category (1995) or had a more even distribution among categories (1997, 1998).

Four-site comparisons.—All four study sites were monitored in the winter of 1998–1999, allowing comparison of regional differences in tortoise hibernation characteristics. There were significant differences in the beginning of hibernation among sites ($F_{3,21} = 10.10$; $P = 0.003$; Fig. 3). Tortoises at Bird Spring Valley (onset date = 15 Oct. ± 1 SD = 15 d) entered hibernation earlier than tortoises at either Lake Mead (10 Nov. ± 1 SD = 7 d) or Littlefield (11 Nov. ± 1 SD = 11 d). The onset date for tortoises at City Creek (25 Oct. ± 1 SD = 6 d) did not differ significantly from the onset dates at the other sites.

There were also significant differences in the duration of hibernation among sites ($F_{3,15} = 5.96$; $P < 0.007$; Fig. 3). The animals at Lake Mead (114 ± 1 SD = 18 days) and Littlefield (115 ± 1 SD = 14 days) hibernated for significantly fewer days than animals at City Creek (146 ± 1 SD = 13 days). Hibernation duration at Bird

TABLE 2. THE NUMBER OF ANIMALS IN EACH TEMPERATURE BUFFERING CATEGORY FOR THE HIBERNACULA SELECTED BY ANIMALS AT CITY CREEK (CC) AND LITTLEFIELD (LF) SITES FOR THE FOUR WINTERS (1995–1998).

Year/site	High (*n*)	Medium (*n*)	Low (*n*)	*P*
1995				
CC	0	7	2	0.01
LF	2	0	2	
1996				
CC	0	8	2	1.0
LF	0	5	1	
1997				
CC	0	10	0	0.035
LF	3	6	2	
1998				
CC	0	6	0	0.044
LF	0	4	5	

Spring Valley (131 ± 1 SD = 7.7 days) did not differ significantly from the other sites. The four study sites did not differ in termination date for hibernation ($F_{3,17}$ = 1.40; P = 0.28; Fig. 3). The termination dates ranged from 11 February to 16 April 1999. There were no differences among sites in the average hibernation temperatures ($F_{3,23}$ = 1.61; P = 0.21), minimum temperatures ($F_{3,23}$ = 0.87; P = 0.76), or mid hibernation temperatures ($F_{3,21}$ = 1.23; P = 0.32).

TABLE 3. THE NUMBER OF ANIMALS IN EACH TEMPERATURE BUFFERING CATEGORY FOR THE HIBERNACULA SELECTED BY ANIMALS AT CITY CREEK (CC), LITTLEFIELD (LF), BIRD SPRING VALLEY (BSV), AND LAKE MEAD (LM) FOR THE WINTER OF 1998–1999.

Site	High	Medium	Low
CC	0	6	0
BSV	0	4	3
LF	0	4	5
LM	0	4	5

Fifty-eight percent of the hibernacula provided medium buffering from thermal environments, while 42% had low buffering, and none provided high levels of buffering. The distribution of animals in each of these patterns did not differ among the four sites for this year (P = 0.12; Table 3). Animals at the sites were relatively evenly distributed between medium and low buffering patterns, with the exception of tor-

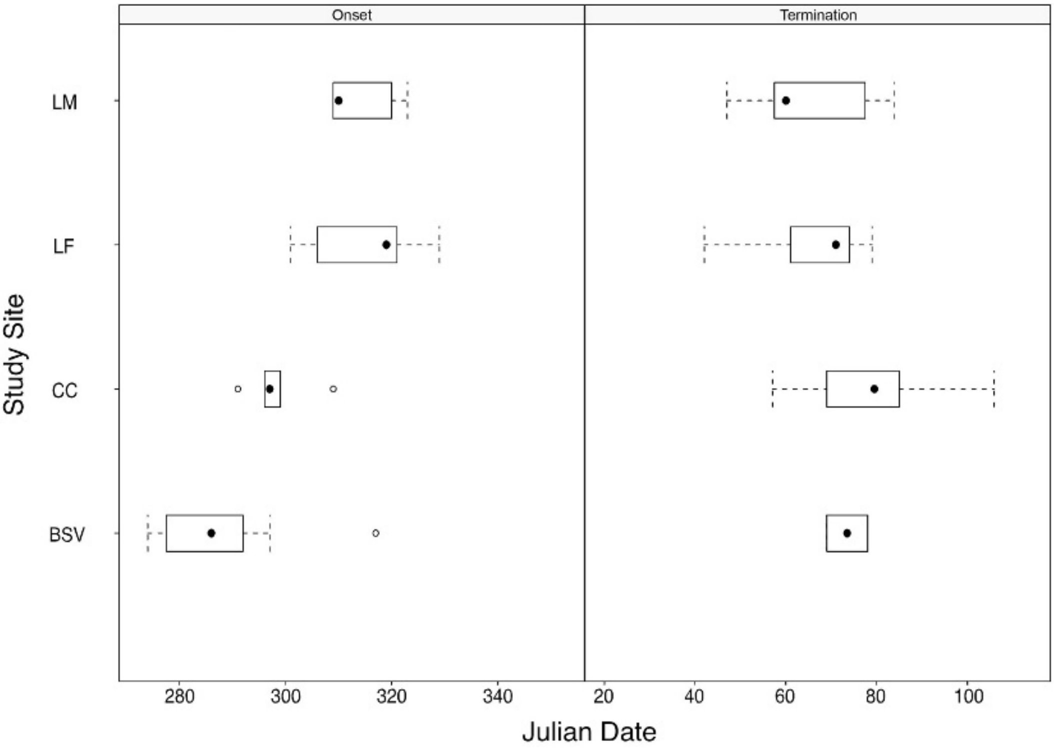

Fig. 3. Onset, duration, and termination of hibernation at the City Creek, Littlefield, Lake Mead, and Bird Spring Valley sites for the winter of 1998–1999. See Fig. 1 for figure explanation.

toises at the City Creek site, at which all animals were categorized as medium.

Meteorological data.—Average air temperatures near the City Creek site indicated differences among years in the temperatures during the fall when tortoises are entering hibernation, and during the spring when animals are terminating hibernation, which were the two periods of specific interest to this study. The two warmest fall periods were during the fall of 1995 and 1997, while the fall months of 1996 and 1998, in contrast, were cooler by about 10 C. Spring temperatures also differed by about 10 C among years during the spring months of March and April when tortoises are typically exiting hibernation. Data for the Littlefield site were available from the spring of 1997 and later. This site had warmer and more consistent temperatures than the City Creek site. A regression analysis of the average date of entry into hibernation at City Creek as a function of the average October air temperatures yielded a non-significant correlation of these two variables ($r = 0.74$; $F_{1,3} = 2.5$; $P = 0.26$). There were not sufficient climate data available to include Littlefield in the analysis. A mixed model analysis of termination date versus average air temperatures in March with Site entered as a random effect to account for repeated measurements was non-significant ($F_{2,6} = 1.5$; $P = 0.33$).

Average air temperatures among the four sites during the 1998–1999 hibernation season differed among sites by as much as 10 C in the fall, but only by about 5 C during the spring months. A regression analysis of onset date as a function of average October temperatures yielded a non-significant correlation between the two variables ($r = 0.70$; $F_{1,3} = 1.9$; $P = 0.3$). A similar analysis of termination date on average March air temperatures yielded a non-significant correlation ($r = 0.46$; $F_{1,3} = 0.54$; $P = 0.54$).

DISCUSSION

There was great individual variation in the timing and duration of hibernation. Exogenous mechanisms did not appear to dictate hibernation patterns at any site or within any year. This leads us to question whether exogenous cues drive hibernation behavior at a population level for this species, or if hibernation behavior is more likely driven by the endogenous conditions of the individuals in association with broad scale seasonal changes in climate.

Among all of our sites and for all years of our study, there was great individual variation in the onset date of hibernation. The onset of hibernation was only weakly correlated with interannual temperature variation, with cooler temperatures associated with earlier onset of hibernation. Onset dates for both the City Creek and Littlefield sites combined were earlier in 1996 than in 1995, which corresponded with an average air temperature in the fall that was 10 C cooler at City Creek, but no significant correlation between onset of hibernation and average October temperatures for 1995–1998 at City Creek was observed. When all four sites were compared within a single year, tortoises appeared to enter hibernation earlier at the sites with cooler fall temperatures, which is consistent with earlier observations (Woodbury and Hardy, 1948; Rautenstrauch et al., 1998). However, this tendency was not statistically significant.

Decreases in air or ground temperature in the fall are the most frequently suggested cue for the onset of hibernation (Gregory, 1982). For example, tortoises were observed to begin hibernation in Kern County, California, when surface temperatures fell below 20 C (Voigt, 1972). We found that daily averages of soil surface temperature at the Bird Spring Valley site fell below 20 C on 27 September 1998, and the first tortoise entered hibernation three days later. However, the last tortoise entered hibernation at the site on 13 November; at that time the temperature of the surface had fallen to approximately 12 C. Thus, soil surface temperature did not appear to be a strong cue driving the onset of hibernation.

Other studies on hibernation in snakes (Viitanen, 1967; Aleksiuk, 1976; Sexton and Hunt, 1980) suggest that reversals in the soil temperature gradient from surface to deep burrow temperature may cue the onset of, and emergence from, hibernation. We also observed tortoises entering hibernation when surface soil temperatures fell below deep soil temperatures; however, the onset of hibernation ranged over a 44-day period, suggesting that this cue has a very weak influence at best.

Increasing photoperiod is hypothesized as an exogenous cue for the emergence of animals from hibernation (Gregory, 1982). During the 35-day range over which individuals terminated hibernation in the spring, the photoperiod would have become approximately 1.5 hours longer. If photoperiod were an important cue for terminating hibernation, we would expect tighter correlation of the termination dates among individuals.

Surface temperatures of the substratum have also been suggested as a cue that influences the timing of emergence. For example, Desert Tortoises in the west Mojave reportedly did not emerge from hibernation until surface temperatures reached 20 C (Voigt, 1972). Moreover, *Terrapene carolina* and *T. ornata* in Missouri reportedly emerge from hibernation after five consecutive days of subsurface (10–20 cm) temperatures of 7 C or higher (Grobman, 1990). We did not observe a relationship between subsurface temperatures and the termination of hibernation at our sites.

Differences between air and surface temperatures in the fall and the spring have also been suggested as a cue for animals to begin or end hibernation (Sexton and Hunt, 1980; Gregory, 1982). However, to make such measurements, hibernating Desert Tortoises would be required to approach the surface and ''test'' the temperature for comparison with deep temperatures, and our results indicate no such behavior. For example, the animals at Littlefield that were in highly buffered hibernacula had no variation in body temperature while hibernating, not even just before they emerged (Fig. 2A). Thus, these animals were not apparently experiencing any external cues and were not sampling the environment, yet they emerged from hibernation at about the same time as other animals. We found that the dates of emergence from hibernation were not statistically correlated with the spring air temperatures at City Creek and Littlefield, with emergence date varying by 35 days at the sites. The average termination date was highly variable and not statistically different among the four study sites during the winter of 1998.

While there were large differences in the air temperatures at the four sites among years, the hibernacula chosen by the tortoises had similar thermal properties, and the average hibernation temperatures were well above outside air temperatures. It should be noted that tortoises chose one of the warmest microclimates in the environment for hibernation, which reduces the likelihood that hibernation is strictly an energy conservation strategy for these animals. Hibernating Desert Tortoises at Rock Valley, Nevada, had a similar duration as found in this study and had low metabolic costs and almost no loss of body mass during hibernation (Nagy and Medica, 1986), which is consistent with other reports for this species (Peterson, 1996; Henen et al., 1998). Tortoises in sites that had colder climates sought shelters that were deeper, and therefore had more stable temperatures as they were more buffered from the environment (Woodbury and Hardy, 1948). Some of the animals at the Littlefield site had body temperatures that had almost no fluctuation, not only on a daily basis, but also over the course of the entire winter.

The temperatures of reptile hibernacula have been previously reported to range between 1 and 15 C (Gregory, 1982). Our data generally fall within this range; however, some individuals chose hibernacula that had temperatures above it. The mean minimum and maximum hibernation temperatures in our study were similar to those observed in the San Pedro Valley, Arizona (Bailey et al., 1995). The female tortoises in Arizona, however, had lower minimum temperatures than did males, while there were no apparent differences in hibernation temperatures between the sexes of our study animals.

Our ability to quantify environmental variability and animal behavior has increased dramatically due to advances in micro-technology. The application of small temperature loggers allowed us to thoroughly examine hibernation behavior and temperatures and to test whether exogenous cues are likely driving hibernation behavior in Desert Tortoises. We found that the timing of hibernation behavior was sufficiently variable that we doubt this behavior is driven predominantly by exogenous cues. Hibernation may prevent tortoises from being exposed to extreme temperatures and potentially lethal ones in the winter, but the onset of hibernation, while variable within a site, was certainly always early enough to avoid this problem at our sites. It may be that endogenous conditions are more important drivers of hibernation than exogenous cues for this species.

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EXHIBIT 456

Carl H. Ernst and
Jeffrey E. Lovich

Turtles of the United States and Canada

SECOND EDITION

REVISED AND UPDATED
WITH NEW SPECIES NAMES

Gopherus agassizii (Cooper, 1863)

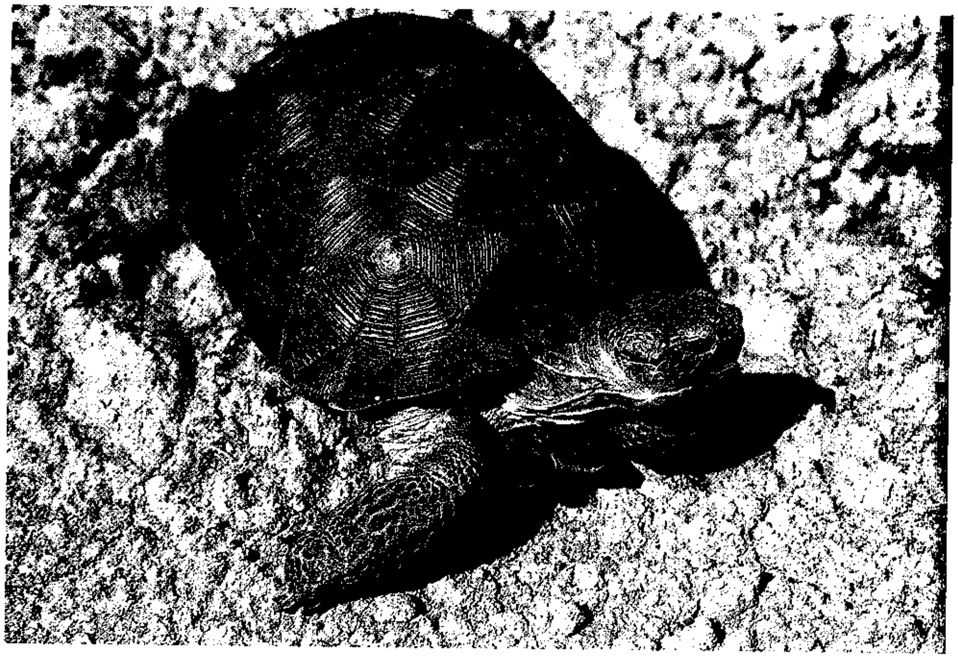
Desert Tortoise

After desert tortoises north and west of the Colorado River were protected under the ESA in 1989, there was a huge increase in the funding available to study the biology of the species and reasons for its decline. Almost two decades later, the desert tortoise is one of the most studied turtles in the United States. Unfortunately, the investment, estimated to exceed $100 million since the species was listed under the ESA, has not resulted in recovery of the species to date. Most of what we know about this species comes from research conducted in California; generalizations in our chapter usually apply to these tortoises. When data are available for other states, we so indicate, because desert tortoise populations are highly variable in terms of their behavior, ecology, and genetic structure. There may even be more than one species involved in what is currently recognized as *Gopherus agassizii.*

RECOGNITION: *Gopherus agassizii* is the largest terrestrial turtle in the United States, reaching a SCL_{max} of at least 38.1 cm (Stebbins 2003). It has large, elephantine hind feet, shovel-like forefeet, and a gular projection on its plastron. Its rough, ridged, but keelless carapace is oblong and highest behind the middle; the rear rim is serrated, and the marginals above the hind limbs are flared. It is black to tan to olive, and often the centers of the scutes are brownish or orangish, particularly in younger individuals. The bridge is well developed and has a single axillary scute. The plastron is large and hingeless; its elongated gular scutes project anteriorly and may bend upward. The plastral scutes are black to tan or olive, some may have yellowish centers. The skin of the limbs is brown, that of the limb sockets and neck yellowish; the head is usually tan but may be reddish brown. The head is somewhat rounded, and the crushing ridges of the upper jaws form less than a 65° angle with each other. Well-developed mental glands are present beneath the chin, and two to five rostral pores lie on the internarial region (Winokur and Legler 1974, 1975). The iris usually is greenish yellow. The forefeet and hind feet are about the same size; the distance from the base of the first claw to the base of the fourth on the forefoot approximately equals the same measurement on the hind foot. The toes are not webbed, and a single large femoral spur is present. Sexually dimorphic size data for the Mojave and Sonoran Deserts are summarized by Germano (1994a).

Males are usually larger (SCL_{max}, 38.1 cm) than females (SCL_{max}, 28.7 cm; Averill-Murray and Klug 1999); males have longer, thicker tails, longer gular projections, and more massive claws than females and have concave plastra. Male mental glands are larger and more complex than those of females, and their secretions may be important in sex recognition (Bulova 1997, Winokur and Legler 1975).

KARYOTYPE: There are 52 diploid chromosomes (26 macrochromosomes and 26 microchromosomes): 20 metacentric and submetacentric, 10 subtelocentric, and 22 acrocentric and telocentric (Dowler and Bickham 1982, Stock 1972).



Gopherus agassizii
(R. W. Barbour)

Distribution of *Gopherus agassizii*

FOSSIL RECORD: Pliocene (Blancan) and Pleistocene (Irvingtonian) remains have been recovered in California (McCord 2002), and Pleistocene (Rancholabrean) fossils of *Gopherus agassizii* have been found in Arizona (Mead 1981, Mead et al. 1984, Van Devender and Mead 1978, Van Devender et al. 1977), California (Brattstrom 1953b, 1955a, 1958; Miller 1942), Nevada (Brattstrom 1954), and New Mexico (Brattstrom 1961, 1964; Holman 1970; Van Devender et al. 1976). In addition, Brattstrom (1955b) reported a fossil tortoise from the Rancholabrean of Cochise County, Arizona, identified only to the genus *Gopherus*. McCord (2002) and Van Devender and Moodie (1977) have summarized the fossil record of the species. Remains of the desert tortoise have also been found at archaeological sites in Arizona, southern California, and southern Nevada; apparently some Native Americans used it for food and medicine and in various rituals and ceremonies (Nabhan 2002, Schneider and Everson 1989).

DISTRIBUTION: The main range of *G. agassizii* extends from southern Nevada and extreme southwestern Utah southward through southeastern California, southwestern Arizona (Hulse and Middendorf 1979), and western Sonora (including Tiburón Island in the Gulf of California) to northwestern Sinaloa (Patterson 1982) and just barely into southwestern Chihuahua (Smith and Chizar 2004), Mexico. This is a more or less continuous latitudinal distribution of about 1,000 km and covers the broadest range of habitats and biotic regions inhabited by any North American tortoise (Germano et al. 1994). Ottley and Velázques Solis (1989) reported it from Baja California, but these records were questioned by Bury et al. (2002) and by Crumly and Grismer (1994).

GEOGRAPHIC VARIATION: No subspecies of *Gopherus agassizii* have been designated, but there is substantial geographic variation in tortoise habitat, ecology, behavior, morphology, and genetics (Berry et al. 2002a). Variation occurs among populations in allozymes, plasma proteins markers, and mtDNA (Glenn et al. 1990, Lamb et al. 1989, Rainboth et al. 1989). In southern Nevada, there is good concordance between ecologically defined desert wildlife management areas (USFWS 1994) and genetic variation (Britten et al. 1997). Allozyme variation, as quantified by measures of genetic distance, is not significant between desert tortoises from the western Mojave Desert (Kramer Hills) and those from the eastern Mojave Desert (Chemehuevi Valley), California (Rainboth et al. 1989). However, other authors have noted significant genetic variation.

Lamb et al. (1989) identified five different mtDNA clones. The first major assemblage consists of three closely related clones (a1–a3) confined to, and fixed, in populations north and west of the Colorado River. The most common genotype, a1, is found throughout the Colorado and Mojave Deserts in California and extends into southern Nevada along the Piute Valley. Clones a2 and a3 are restricted to tortoises living in the northeastern Mojave Desert and are geographically coincident with the northern distributional limits of the species. A second major assemblage, clone a4, occurs from west central and southern Arizona to central

Sonora. Tortoises from southern Sonora have genotype a5, the third major assemblage. A plasma protein marker resembling albumin was found to be polymorphic for electromorphs in northern Mojave Desert populations, while Sonoran Desert populations to the south were monomorphic (Glenn et al., 1990). These results support those previously reported by Lamb et al. (1989), which show divergence between desert tortoise populations on either side of the Colorado River, with the exception of the Black Mountains of Arizona, where the predominant genotype is Mojavean (Lamb and McLuckie 2002, McLuckie et al. 1999), not Sonoran.

Based on data estimated from "molecular clock" data, Lamb and McLuckie (2002) suggest that the separation between Mojave and Sonoran tortoises occurred about 5 million years ago, perhaps at the time of the origin of the Bouse Formation, a marine embayment that formed in what is now the Colorado River valley at the Miocene–Pliocene boundary. This agrees with the 5.5-million-year separation proposed by Avise et al. (1992). Additional evidence of differentiation between Mojave and Sonoran Desert tortoises was suggested by an analysis of microsatellite loci by Edwards et al. (2003).

The interpretation of Lamb and McLuckie (2002) was challenged by Van Devender (2002a), who noted that there were no climatic changes associated with the origin of the Bouse Formation that would have driven differentiation between Mojave and Sonoran tortoises. Instead, he postulated that differences between "Mojave" and "Sonoran" desert tortoises are based on newly derived characters in the Mojave form that evolved after the development of a winter rainfall climate at the end of the Pleistocene, perhaps as early as 2.4 million years ago. Evidence in support of this hypothesis is provided by the fact that there are no known fossil records that can be unequivocally assigned to *G. agassizii* from before 34,000 years ago. However, recent reports of Pliocene (Blancan) and Pleistocene (Irvingtonian) material from Anza-Borrego Desert State Park in California (where tortoises do not occur naturally today) suggest that the fossil record might be a little older (McCord 2002). The evolution of Mojave tortoises from Sonoran stock suggests that Mojave tortoises are tenuous relicts poorly adapted (physiologically) to life in the more arid Mojave Desert (Morafka and Berry 2002, Peterson 1996a; see also Remarks).

The general agreement between molecular-based studies and traditional morphometric analysis (Weinstein and Berry 1987) suggests that the desert tortoise is made up of more than one taxonomic unit. Lamb and McLuckie (2002) suggested that the Mojave, Sonoran, and Sinaloan tortoise populations were sufficiently distinctive to qualify as evolutionarily significant units or valid geographic races. Similarly, Berry et al. (2002a) noted that many populations of tortoises in the *G. agassizii–G. berlandieri* complex exhibit enough variation to be considered species, subspecies, distinct population segments, evolutionarily significant units, or management units. Each of these designations has its own definitions and presents its own challenges regarding taxonomy and the resolution of phylogenetic relationships. Differences among populations are manifested in morphological variation as well. Mojave tortoises are wider than Sonoran or Sinaloan tortoises, with the latter the narrowest of the group. Mojave tortoises are also more domed than Sinaloan tortoises and have longer gular projections than Sonoran tortoises but not Sinaloan tortoises (Germano 1993). Based on allozyme analysis, no fixed differences were observed between *G. agassizii* and *G. berlandieri*, and the two may be allopatric populations of *G. agassizii* according to Morafka et al. (1994). The 500-km gap between the two closest portions of the range of these species was reduced or closed about 20,000 years ago, further supporting their hypothesis.

A tortoise from Baja California was described as a new taxon, *Xerobates lepidocephalus* (Ottley and Velázques Solis 1989), but Crumly and Grismer (1994) have shown that the adult female holotype is a *Gopherus agassizii.*

CONFUSING SPECIES: Within its United States range, only the terrestrial *Terrapene ornata* and the aquatic *Kinosternon sonoriense, K. arizonense, K. flavescens,* and *Actinemys marmorata* could be confused with a young desert tortoise. However, each of the first four has a hinged plastron and lacks a gular projection. The latter differs from the desert tortoise in having a relatively flat shell profile, a mottled head, and webbed feet.

HABITAT: Desert tortoise habitat in the United States is broadly divided between two desert ecosystems, those of the Mojave and Sonoran Deserts. The Mojave Desert is situated between the Sonoran Desert to the east and south and the Great Basin Desert to the north. The Mojave receives most of its precipitation in the form of winter frontal systems, particularly in its western portion, and its vegetation is characterized as "desert scrub" with comparatively few cacti (Vasek and Barbour 1977). In contrast, the Sonoran Desert experiences both winter frontal and summer monsoonal precipitation, and its vegetation is characterized as subtropical desert scrub, with a remarkable diversity of cacti and other perennial plants (Burk 1977). The portion of the Sonoran Desert located in California is frequently referred to as the Colorado Desert and is much drier and lower than other parts of the Sonoran Desert, and this affects tortoise distribution and abundance. Differences between the Sonoran and Mojave Deserts translate into significant differences in tortoise behavior, reproduction, food plants, and most other aspects of their ecology.

Desert tortoises occasionally occupy some other habitat types, perhaps as an accident of wandering, or even of transport by humans, past (Schneider and Everson 1989) or present. Van Devender (2002b) reported a population in Arizona at 1,520 m in oak woodland habitat, and Aslan et al. (2003) found a single animal in a ponderosa pine–dominated coniferous forest in a roadless wilderness area of the Rincon Mountains of southern Arizona. Van Devender also cited references supporting their occasional occurrence elsewhere in Arizona in desert grassland or Chihuahuan desert scrub habitats. Farther south, in Sonora and Sinaloa, Mexico, the "desert" tortoise occupies tropical thorn scrub and deciduous tropical forest ecosystems that do not occur in the United States.

The desert tortoise inhabits desert alluvial fans (bajadas), washes, canyon bottoms, and hillsides with rocky, sandy, or gravelly soil, depending on location. It occurs at elevations of 1,500–1,600 m (Bury et al. 1994, Van Devender 2002b) and possibly more than 2,000 m (Aslan et al. 2003, Luckenbach 1982), but these must be rare occurrences: in general, tortoises occupy lower elevations. The particular habitat types utilized vary geographically, gradually changing from valley bottoms and bajadas in the northern and western portions of the range, notably the Mojave Desert, to rocky slopes in the southern and eastern part of the range, notably in the Sonoran Desert of Arizona (Barrett 1990, Schamberger and Turner 1986). At the Nevada Test Site in the Mojave Desert, tortoises appear to be more abundant in mountainous areas high on alluvial fans and on the lower slopes of mountains (Rautenstrauch and O'Farrell 1998), unlike tortoises of other populations in the Mojave Desert. Similarly, tortoises in the San Bernardino Mountains near Palm Springs, California, occur in a more precipitous landscape than do other nearby populations (Lovich and Daniels 2000).

Often present in desert tortoise habitats, depending on location, are creosote bushes (*Larrea tridentata*), burrobushes (*Ambrosia dumosa*), cheesebushes (*Hymenoclea salsola*), blackbrushes (*Coleogyne ramosissima*), saltbushes (*Atriplex* sp.), hopsage (*Grayia spinosa*), palo verdes (*Cercidium* sp.), ironwoods (*Olynea tesota*), smoke trees (*Psorothamnus spinosus*), annual and perennial grasses, and cacti. Typical of habitats occupied in Arizona are Sonoran upland plant communities on rocky hill slopes dominated by saguaro cacti (*Carnegiea gigantea*) and foothill palo verdes (*Cercidium microphylla*). Distance sampling in the Ironwood Forest National Monument in Arizona found tortoise sign (shells, burrows, scat) in the following proportion of transects through various habitat types grading from hilly to flat: boulder habitat, 92%; incised washes, 71%; and habitats with neither feature, 25%. The latter habitat included areas up to 1.7 km away from the nearest hill slope (Averill-Murray and Averill-Murray 2005).

Although a wide range of habitats are occupied in the Mojave Desert, the "typical" habitat in much of California is found in valley bottoms dominated by creosote bushes (*Larrea tridentata*) and burrobushes (*Ambrosia dumosa*). Modeling of desert tortoise habitat at the Army's National Training Center in the Mojave Desert of California suggested that tortoises there tend to occur on southwest exposures with loamy soils, while they avoid stony soils, northern exposures, and areas with low plant cover (Andersen et al. 2000). The spatial distribution of desert tortoises in relation to plant communities is not random (Baxter 1988). High-diversity plant ecotones and communities, and possibly soil characteristics, are important features in determining tortoise densities (Wilson and Stager 1992). At the Nevada Test Site, tortoise sign is more abundant on the slopes of carbonate mountains than on those of mountains of volcanic origin. Again, creosote bush associations are important determinates of tortoise sign, with less sign found in areas dominated by blackbrush (*Coleogyne ramosissima*) (Rautenstrauch and O'Farrell 1998). Although *Terrapene ornata* may occur with *G. agassizii* at some Arizona localities, no other North American turtle shares the more severe microhabitats occupied by this species.

The soil characteristics that may have affected the habitat quality of tortoise populations in Piute Valley, Nevada, were summarized by Wilson and Stager (1992). Soil consistency at a depth of 0–40 inches is important, because tortoises are burrowers. Soil with a high level of structural strength, hardpan (caliche layers), or coarse rock fragments (clasts) may impede digging (the latter may also impede mobility aboveground). The soil water capacity available can be a limiting factor due to either drought or flooding, and it can be difficult to construct and maintain burrows in loose soil with low water capacity. Soil salinity was also considered due to its possible relationship with the water balance of the tortoise, especially due to the saline content of tortoise forage. The mean annual soil temperature at a depth of 20 inches (high, 15–22°C; low, 8–15°C) was also examined. When these soil characteristics were applied to soils in the study area, the highest ratings of habitat quality corresponded with the highest densities of tortoises. The plant community in Piute Valley is made up of creosote bushes (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*), with a herbaceous understory that is predominantly a mixture of introduced and native annual forbs and grasses.

BEHAVIOR: *Gopherus agassizii* has a relatively long annual period of activity, usually emerging from hibernation in February–late April and retiring for the winter in late September–November. Averill-Murray et al. (2002a) summarized data indicating that male tortoises emerge from hibernation about a month later than females in several populations in Arizona. This cycle depends on both latitude and elevation, as well as precipitation patterns, varying between the Mojave and Sonoran Deserts. Most surface activity occurs from late April to June–July and, at some localities, from late August to September. In Mexico, the period of greatest surface activity seems to occur in late summer and early fall (Osorio and Bury 1982). In Arizona, peak activity is related to the summer monsoon, which traditionally runs from 4 July to 1 September (Averill-Murray et al. 2002a).

In the warm season, the daily activity of *G. agassizii* is governed largely by temperature, although it becomes active during most diurnal rainstorms. It forages for a short period after sunrise and again in the late afternoon. Between active periods, the tortoise rests in its burrow. This pattern is followed over most of the range, but in California Luckenbach (1982) found that the period of activity varied according to the season. During the 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 above-ground activities from about 1000 to 1900 hours. This pattern grades into a unimodal late morning–sunset pattern again in the fall (September–November). The desert tortoise is diurnal except, perhaps, during rare rainstorms that may trigger nocturnal emergence (Luckenbach 1982).

The activity and behavior of desert tortoises in 4.1-ha pens was studied by Ruby et al. (1994a) near Las Vegas, Nevada, under seminatural conditions. The various pens received different levels of supplemental food and water. Supplemented pens were seeded with forbs or planted with sod and then irrigated with sprinklers; some plots received more water than others, creating fully supplemented and intermediate conditions. Unsupplemented pens did not receive water. Tortoises, especially males, moved farther during observation in unsupplemented plots than in supplemented ones, although there were no differences in feeding rates among treatments, except related to rainfall patterns. The morning activity period was shorter in unsupplemented pens. Home ranges were not significantly different between treatments. Overall, the authors concluded that under environmentally stressful conditions, tortoises spend less time aboveground but compensate by increasing their movement and feeding while active.

Some desert tortoises first become active at ATs of 15°C; activity gradually increased with rising temperature, until at about 26.7–29.4°C all were active (Woodbury and Hardy 1948). McGinnis and Voigt (1971) reported that the tortoises' deep core BTs may be up to 10°C cooler than that of the shell surface, and they thought that the carapace scutes act as a buffer against solar radiation. Brattstrom (1965) and McGinnis and Voigt (1971) found that the BTs of active *G. agassizii* were 15.0–38.3°C and the CT_{max} was 39.5°C; however, Hutchison et al. (1966) found that a *G. agassizii* lost its righting ability at 39.0°C and that its CT_{max} was 43.1°C. (An individual kept on its back in direct sunlight will die in a short time, but tortoises can often right themselves by using their head, neck, and forelimbs.) Berry and Turner (1984) observed that tortoises less than 6.0 cm in SCL were active at significantly lower ATs than larger individuals. ITs do not affect the temperature selected by hatchlings in thermal gradients at one week or 40 days after hatching (J. R. Spotila et al. 1994).

Voigt (1975) measured the heating and cooling rates of desert tortoises. Heating rates in the field were as much as 10 times faster than cooling rates, and heart rates during heating were significantly faster than during cooling at any particular BT. Difference in the rates of heating and cooling presumably allow the maintenance of suitable BTs for digestive and reproductive activities for a period after the tortoise has retreated into its burrow. Measurements of O_2 consumption were taken by Naegle and Bradley (1975) over ETs of 8–42°C; the Q_{10} values at 10–20°C, 20–30°C, and 30–40°C were 3.2, 2.3, and 1.8, respectively, and tortoises <500 g had significantly higher O_2 consumption rates than those >500 g.

Some of the best available information on the thermal ecology of the desert tortoise is provided by Zimmerman et al. (1994). They used aluminum models of tortoises that had the same thermal characteristics as live tortoises to measure operative temperatures (the estimated range of possible BTs) during the period from July to October. Periods of surface inactivity (in penned and free-ranging tortoises observed during their study) generally coincided with ATs >45°C. The tortoises entered their burrows in the later morning, when ATs were between 40 and 45°C, and they emerged from their burrows in the afternoon, when ATs were between 45 and 50°C. This range encompasses temperatures that are critical (43.1°C; Hutchison et al. 1966), but when tortoises emerge from their burrows in the afternoon, their BTs are lower than the ETs, which are falling, and their thermal inertia (due to the fact that it takes time to heat up a relatively large cool object) protects them.

Besides overheating, the other major environmental problems of *G. agassizii* are water retention and the difficulty of maintaining their salt balance. Desert tortoises lose water by evaporation and urination. Some water is always lost by evaporation from the lungs; however, the skin permits the passage of less water than does that of turtles in damper climates (Schmidt-Nielsen and Bentley 1966). Desert tortoises' bladders are large and bilobed, functioning as a storage organ for potassium and nitrogenous waste, as well as a water reservoir for reabsorption of water (Jørgensen 1998). Dantzler and Schmidt-Nielsen (1966) showed that the urinary bladder of the desert tortoise is more permeable to water than that of freshwater turtles and that the tortoise excretes nitrogenous wastes in the semisolid form of urates, including uric acid that precipitates with ammonium, potassium, nitrogen, and sodium (Oftedal 2002). Dissolved potassium is the major ion in urine, with large amounts in precipitated urates (Jørgensen 1998).

When water is available, tortoises excrete liquid urine, but they are able to go for months without discharging water from the bladder. Urine density relative to water is lowest in July during peak rainfall (in the eastern part of the range) and increases thereafter (Christopher et al. 1994). Because most food plants contain high levels of potassium and low levels of protein (nitrogen), tortoises would lose more water in urine than they obtain in food if they relied on urine excretion only. By storing precipitates such as potassium in the bladder and voiding infrequently, tortoises successfully excrete potassium without excess water loss. The conflicting demands of excreting excess potassium and recycling low levels of nitrogen can cause problems. For example, tortoises fed high-potassium diets are unable to retain nitrogen for growth even on a high-protein diet. As a result, tortoises face a difficult task of balancing their needs for one potentially toxic resource (potassium) and two resources that are scarce in their habitat and food (water and protein) (Oftedal 2002).

A potassium excretion potential (PEP) index is a method of measuring the impact of varying diets on animals' osmoregulation and protein assimilation (Oftedal 2002). Peterson (1996a) demonstrated that desert tortoises' urine osmolality increases dramatically during the foraging season, due primarily to increases in soluble potassium. A positive PEP index indicates that there is more than enough water and protein in the food for a tortoise to excrete excess potassium, while a negative PEP index implies that there are inadequate amounts of water and nitrogen in food for the tortoise to excrete excess potassium. The index provides a tool to test the hypothesis that tortoises avoid low–PEP index foods unless they can find other sources of water and protein. Major tortoise foods with high PEP indexes include evening primroses (Onagraceae), filaree (Geraniaceae), legumes (Fabaceae), mustards (Brassicaceae), and spurges (Euphorbiaceae), but the index may fall based on changing plant phenology. There is some evidence that tortoises selectively forage for high-PEP plants, at least in wet years.

A critical test of the PEP hypothesis was provided by Oftedal et al. (2002) using radio-telemetered juvenile tortoises in naturally vegetated enclosures in the central Mojave Desert of California. An El Niño year ensured the germination of large numbers of food plants during the study. The average SCL of the juveniles was 8.1 cm, and they ranged from five to seven years of age. Plants eaten by the tortoises had, on average, higher levels of moisture content and protein content and higher PEP indexes than the plants they bypassed but did not have lower levels of potassium. Part of this was due to low ingestion of the exotic grass *Schismus* sp., which accounted for about 86% of the biomass on their foraging trails. Avery and Neibergs (1997) also noted that tortoises ate but did not prefer the exotic plants *Schismus barbatus* and *Erodium cicutarium*. Removing *S. barbatus* from the analysis demonstrated that the plants eaten exhibited higher average PEP indexes and levels of protein but were lower in water content and potassium than the plants not eaten. Tortoises also selected parts of the four preferred plant species, choosing leaves in more than 70% of the observed bites. Leaves were higher in PEP index, water, and protein and lower in potassium than the parts of the plants that were not eaten. Oftedal et al. (2002) concluded that juvenile tortoises are able to select food plants and parts with high nutritional quality.

July thunderstorms in Nevada trigger emergence from estivation, and the tortoises drink rainwater, void concentrated urine, accumulate dilute urine, restore normal plasma osmotic concentration, resume feeding on the still-dry grasses and forbs, and accumulate surplus energy (Nagy and Medica 1986, Oftedal 2002, Peterson 1996b, Van Devender 2002b). Consumption of dry plants is necessary to achieve energy balance or surplus because eating spring annuals alone does not provide the energy needed to balance energy expenditures (Peterson 1996b), but dry food plants do not allow juvenile tortoises to achieve water balance (Nagy et al. 1997). The availability of water is essential for digestion (Henen 2002a). However, the tortoises' BM declines during this period due to negative water balance, and the osmotic concentration in bladder urine increases. The average potassium concentration in the urine of captive tortoises fed high-potassium diets (3.7% potassium dry matter) is 163 mmol/L (Oftedal et al. 2002). More rain in September relieves osmotic stress as tortoises again drink, urinate, and store dilute water. When tortoises are kept in captivity and provided with supplemental water, they experience stress-related changes in blood chemistry that mirror those of free-ranging tortoises without access to supplemental water. Enclosing tortoises in pens at higher densities than normal may be the reason for the observed stress (O'Connor et al. 1994a).

Desert tortoises' energy balance remains strongly positive until they begin feeding on succulent new sprouts of annual plants germinated in late September, and the tortoises return to a springlike physiological condition in mid-November when they begin hibernation. Tortoises apparently relinquish the maintenance of internal homeostasis on a daily basis during most of the year while tolerating large imbalances in their water, salt, and energy budgets (Henen 2002a, Nagy and Medica 1986). This ability lets them exploit resources that are only periodically available (Henen 2002a) while balancing their water and salt budgets on an annual basis and showing an energy profit. *G. agassizii* and other turtles are low-energy specialists. Peterson (1994a, 1996b) estimated that the amount of energy expended by a 3-kg desert tortoise in a full year would sustain a 3-kg mammal for only 3.5 days! The field metabolic rates of juvenile tortoises are similar to those of adults in the spring, when water is available, and about half those of adults in the dry spring and summer seasons (Brown et al. 2005, Nagy 2000, Nagy et al. 1997).

Desert tortoises are capable of drinking large amounts of water when it is available, and this is periodically necessary for their survival, because over most of their range, rains are infrequent and unpredictable; these tortoises occasionally construct small catchment basins during showers and thunderstorms that are capable of holding water for up to six hours (Auffenberg 1969; Medica et al. 1980; Nagy 1988; Nagy and Medica 1977, 1986; Peterson 1996b; Woodbury and Hardy 1948). Nagy and Medica (1986) reported that individuals increased their BM almost 20% by drinking, and Miller (1932) reported that they increased it by as much as 43%. The amount of weight gained from drinking depends on the prior osmotic state of the tortoise. Henen (2002a) reported that California females with a mean BM of 1,644 g consumed a mean of up to 536 mL of water, or about 33% of their BM. In contrast, during times of drought, tortoises' BM may decrease 40%, and their total body water content may decline to 60% or less of their BM (Peterson 1996a). Juveniles lose body water at higher rates in the laboratory (0.4–0.8% of BM/day) and in the field (0.7–1.1%) than do adults, which can lose water in the laboratory at 0.17%/day and in the field at 0.1%/day (Wilson et al. 2001). Such high rates of loss compared to those of adults mean that juveniles are very dependent on rainwater and on long humid burrows for survival.

The water economy index measures the ratio of water intake to the field metabolic rate and reflects the amount of water used to produce a given unit of energy processed. Low ratios are reflective of low water requirements as long as the individual is not losing BM. The water economy index for hatchling and one-year-old tortoises in seminatural field enclosures in the west Mojave Desert ranged from 0.009 to 0.55 mL H_2O / kJ (Nagy et al. 1997). High values were observed in the spring, when young tortoises were gaining BM. Nagy et al. (1997) regressed the water economy index on BM change to estimate a steady-state value of 0.29 mL/kJ, a value higher than that of most herbivores and appreciably higher than that of adult desert tortoises (Peterson 1996a). Nagy et al. (1997) concluded that juvenile tortoises may drink rainwater (Wilson et al. 2001) or select succulent foods (Oftedal et al. 2002) to maintain their water balance in the harsh desert environment. Utilization of long burrows with higher humidity (Bulova 2002, Wilson et al. 2001) contributes to their water economy. Reviews of how tortoises deal with variation in water availability in the desert are given by Jørgensen (1998) and Nagy (2003).

Field et al. (2007) conducted a translocation experiment in southern Nevada with tortoises that were kept in seminatural conditions under two water treatments: water-supplemented and nonsupplemented. On the day of their release into the translocation site, all tortoises were soaked in water for 20 minutes. In that short period of time, the average weight gain of tortoises that did not have access to water in their pens prior to soaking was 13.2%. Tortoises in the water-supplemented treatment actually lost an average of 0.25% of their BM, because many voided feces and urine in the tubs of water. When tortoises have access to free water, they have the opportunity to purge their bodies of accumulated urates and regain a positive water balance.

The basic water supply of a wild desert tortoise must often come from food. Henen (2002a) calculated that 77–86% of the water that tortoises obtain comes from drinking free water and from dietary water sources; the dietary water content of food items eaten at Goffs, California, ranged seasonally and by food type, from 0.005 to 11.960 g water / g dry matter.

Nagy and Medica (1977, 1986) reported that tortoises gained weight during the spring while eating 3–4% of their BM in succulent annual plants each day, but by summer their water intake rates dropped from about 25 to 5 mL/day, and their metabolic rates also declined. Studies suggest that during the first two years of life tortoises need about 350 g of plant food, or about 175 g of dry matter, to grow from 34 to 55 g in BM (Nagy et al. 1997). During most of the summer, their daily water turnover rates are very low, 0.36 mL/ 100 g, and only slightly greater than their rates of water metabolic production, 0.31 mL/day (Minnich 1976, 1977). Water losses are minimized in the cool, moist burrows of desert tortoises, and water balance can be achieved during hibernation. Tortoises accumulate fat for hibernation, and this is also a source of metabolic water, albeit a small input (Henen 2002a, 2002b).

An extensive synthesis of energy and water balance in the desert tortoise was provided by Henen (2002a), who summarized much of his earlier research (Henen 1997, Henen et al. 1998) and that of others (Christopher et al. 1999, Dickinson et al. 2002a, Peterson 1996a, 1996b). The desert tortoise has the ability to survive huge variations in energy, water, mineral (electrolytes), and nutrient stores, affecting osmotic state and other physiological parameters. This ability is called anhomeostasis (Peterson 1996a). For example, multiyear studies of water influx rates of males and females reveal that these vary by a factor of 237, while field metabolic rates vary by a factor of 28, according to Henen. Much of this variation is due to year-to-year fluctuations in rainfall and the response of desert tortoises to those fluctuations (Christopher et al. 1999, Dickinson et al. 2002a, Henen et al. 1998, Peterson 1996b). Even when trapped in burrows by rock fragments for nearly 11 months, tortoises have been known to survive without food or water (Christopher 1999). The wide variation of physiological conditions that tortoises can survive would kill many other vertebrates (Peterson 1996a), especially mammals that generally maintain extremely close tolerances for physiological parameters (homeostasis). The ability to relax homeostasis or temporarily abandon it in response to the highly variable environmental conditions of the desert is an important survival adaptation of *G. agassizii.* They take full advantage of critical resources when they are available and conserve them in times of shortage. Female tortoises in California had energy deficits of about 20 kJ/day during the period from August of one year to March of the next year; most of their energy came from lipid and nonlipid energy sources (tortoises use the breakdown of protein to fuel their metabolism during hibernation; Christopher et al. 1994, Peterson 1996a). High lipid storage rates allowed their body lipid concentration to increase from 2 to 8% during the summer of the first year of study. The lipids they stored supported their metabolism during winter dormancy and, along with lipids accrued from spring annuals the next year, resulted in a positive energy balance. Although they had a surplus of energy, their nonlipid stores decreased 21% during this time.

A second dry year of study resulted in low biomass of food plants. Females maintained a balance of lipid, nonlipid, and total body energy by offsetting losses to metabolism during winter dormancy with lipid resources obtained the following spring. Accrual of nonlipid stores in the summer compensated for the loss of nonlipid matter to metabolism and egg production the following spring. Field metabolic rates in the second year were lower than those in the first year, and these savings may have allowed most females to produce eggs in the dry year.

A condition index (CI) defined as the ratio of BM and shell volume (SCL × CH × CW) was calculated by Nagy et al. (2002) for Mojave Desert tortoises. A prime CI was determined based on the highest CI value obtained during the study period (which coincided with above-average rainfall). The mean prime CI was 0.64 g/mL and ranged from 0.6 to 0.7 g/mL. Overall, the prime CI did not vary according to sex, study sites in the eastern and western Mojave Desert, variation in body size of adults, or age. In adult males, there was a relationship between prime CI and increasing BM. As expected, there were seasonal and geographic differences related to the availability of food plants and free water. Hatchlings had very low CIs following five months of drought. CIs based on relationships between weight and length found no significant differences between healthy tortoises and those with upper respiratory tract disease, although unhealthy tortoises weighed about 7% less than healthy tortoises; Jacobson et al. (1993) concluded that predicting health based on this relationship was not possible. Hematocrit or packed blood cell volume is also a poor predictor of physiological state in tortoises, although dehydration increases concentration during drought conditions (Peterson 2002).

Desert tortoises typically begin hibernation in October or November, but some may enter hibernacula as early as late August (Rautenstrauch et al. 1998). The average date that males (5 November) and females (12 November) entered hibernation at three sites in Arizona did not differ significantly (Averill-Murray et al. 2002a). However, in south central Nevada, adult males entered hibernation and were torpid later than adult females, while juveniles emerged earlier than adults (Rautenstrauch et al. 1998). At the Nevada site, 98% of tortoises entered hibernacula by 15 November and 98% remained in hibernation by 15 February. During that period, many of the animals that left their burrows did so after being disturbed by handling, but the tortoise will also bask at the entrance of its den on warm winter days (Repp 1998).

In southwestern Utah, desert tortoises congregated in large communal dens during the winter (Woodbury and Hardy 1948). These were dug as deep as 10 m into gravel banks, and some had multiple openings. As many as 23 tortoises were found in one burrow, and some returned to the same burrow annually. Burrow fidelity spanning six consecutive years has been observed in Arizona (Averill-Murray et al. 2002b), but elsewhere in Arizona, none of the tortoises observed over two years used the same hibernation site in both years (Bailey et al. 1995). Freilich et al. (2000) also reported burrow fidelity in Joshua Tree National Park. Auffenberg (1969) observed that in Pima County, Arizona, individuals often returned year after year to particular hibernacula. These winter burrows were always located well above the floor of arroyos and usually were enlarged ground squirrel burrows. The typical burrow extended just far enough that the rear portion of the tortoise's shell was even with the arroyo wall. This depth was apparently sufficient to shelter the tortoise from the cold night winds but to allow the exposure of part of the shell to the rays of the afternoon sun: the burrows were always located in a south-facing slope, and four or five tortoises sometimes occupied adjacent burrows. Nichols (1953) saw several captives combine their efforts to dig a communal hibernaculum.

In Arizona, females tend to hibernate in shallower burrows than males (Averill-Murray et al. 2002a), with consistently higher (24.5°C versus 18.2°C) but not statistically different maximum temperatures (Bailey et al. 1995). Female hibernation burrows have significantly cooler minimum temperatures (4.3°C) than those of males (9.3°C). Male burrows average 118.3 cm, while those of females average only 24.4 cm. The wide variation of temperatures in female hibernacula is likely due to the shallow, more exposed nature of their burrows. Hibernacula reported by Bailey et al. (1995) were often associated with both living and dead vegetation and packrat (*Neotoma albigula*) nests. The majority of burrows located occurred on steep (>45°) south-facing slopes in soil types including silt, silt with loose gravel, diatomite and/or diatomaceous marl, or layers of well-lithified volcanic ash. Nichols (1957) reported that several young captive tortoises hatched in California did not hibernate during their first winter, but all hibernated the second winter. The overwintering ecology of *G. agassizii* is summarized by Ultsch (2006).

The burrowing habits of tortoises vary geographically. Although tortoises are known to be prodigious burrowers in much of California, Nevada, and Utah, in the Sonoran Desert of Arizona they tend to live in rocky uplands where extensive burrowing might be difficult or unnecessary due to the ready availability of rock shelters (Van Devender 2002b). *G. agassizii* may spend more than 98% of their lives underground (Nagy and Medica 1986), especially in drought years (Oftedal 2002). They construct a burrow that provides a special microhabitat: the humidity is higher, and the temperature is lower and more constant in the burrow than outside it. From 1000 to 1200 hours, the humidity can be significantly higher in burrows than on the surface, while the temperature and predicted loss of water by evaporation are lower. Longer burrows and those with smaller entrances often have greater humidity and lower temperatures than the surface (Bulova 2002), and juveniles confined to shorter, warmer burrows lose BM faster than those in longer, cooler burrows (Wilson et al. 2001). During the winter in the west Mojave Desert, active juvenile tortoises used significantly shorter (mean, 29.4 cm) burrows than inactive juveniles (mean, 60.3 cm) (Wilson et al. 1999a).

Using relative humidity measurements and ETs taken over 24 hours, Bulova predicted that a tortoise using a burrow would lose 4.0–4.7 g H_2O / day, while a tortoise remaining on the surface during the same period would lose 4.6–4.7 g H_2O / day. Because the difference is small, Bulova concluded that burrows were more important for protection from lethal surface temperatures than from dehydration: a tortoise will die faster from overheating than from dehydration. Wilson et al. (2001) studied water loss in hatchling and juvenile tortoises and found that sleeping tortoises lose BM at half the rate of active tortoises, while hibernating tortoises lose water at 5% of the rate of active animals. By retreating into burrows, the tortoises relieve the problems of evaporative water loss and high BT. In extremely hot weather, tortoises may stay in their burrow all day, but they are especially active during rains when the cooler ATs and higher humidity make conditions outside the burrow more tolerable (Bulova 2002).

The tortoise digs by scraping alternately with its forelimbs; when the hole becomes deep enough, the turtle turns around and pushes the dirt out with the sides of its shell. The burrow is dug in dry, gravelly or sandy soil and is often located under a bush in an arroyo bank or at the base of a cliff. In cross-section, it is somewhat semicircular; it may be straight, curved, or forked, and many burrows have enlarged chambers. Although sometimes just long enough to admit the tortoise, it is rarely up to 10 m in length (Woodbury and Hardy 1948).

Several types of burrows are constructed for different reasons, and the type and depth of burrows may be related to soil type and to winter and summer temperature extremes (Berry 1978). Burge (1978) found four types of cover sites in southern Nevada: den, burrow, pallet, and nonburrow. The average density of cover sites used repeatedly (pallets or burrows) was 3.5/ha. Of 783 burrows and pallets, 665 (85%) were in soil with varying amounts of gravel, 564 (72%) were located under shrubs, and 203 (26%) were dug into banks or beds of dry washes. Individual tortoises used 12–25 cover sites/year, and most were used repeatedly.

Dens are horizontal tunnels dug in banks of washes, usually for distances of 2–4.5 m but occasionally for 6–10 m. Summer burrows are scattered over the flats and benches and are dug downward at angles of about 20–40° for a distance of 1.8–2.4 m. Pallets are only about 25 cm to 1.5 m deep. In Sonora, Mexico, Auffenberg (1969) found that the tortoise's summer retreat was most commonly a shallow hollow dug into the base of an arroyo wall; several tortoises may use the same shelter during a single season (Bulova 1994). The lengths of burrows of neonates and juveniles in seminatural enclosures in the west Mojave Desert averaged 52.7 cm and ranged from 5 to 130 cm (Wilson et al. 1999a).

In Utah, woodrats (*Neotoma* sp.) and rattlesnakes (*Crotalus oreganus*) may share winter burrows with desert tortoises (Woodbury and Hardy 1948), and in California, desert tortoise burrows may be shared with other rattlesnakes (*Crotalus ruber, C. scutulatus*) and black widow spiders (*Latrodectus mactans*) (Baxter and Stewart 1986; Lovich, personal observation). Other species observed cohabiting with desert tortoises include western diamondback rattlesnakes (*Crotalus atrox*) (Barrett and Humphrey 1986) and a host of other species, both invertebrates and vertebrates (see Luckenbach 1982). Caliche caves frequented by tortoises in the Sonoran Desert of Arizona may be occupied by Africanized honey bees (*Apis mellifera scutellata*) (Stitt et al. 2004).

The use of shelter sites (burrows, dens, and pallets) in southern Nevada was documented by Bulova (1994). From June to October of one year, 28 radio-tagged tortoises used an average of 9.1 (range, 3–18) different shelters, switched shelters an average of 11.3 (range, 2–32) times, and spent an average of 1.7 (range, 0–20) days in the same shelter. The sexes had seasonal differences, with females using more shelters, switching more often, and moving to more new shelters than males. These differences were not observed in July or October, but in August and September males used more shelters and switched more often than females. There was no significant difference in the length of stay in a burrow between the sexes in any month. When tortoises moved from one shelter site to another, the average distance was 148.9 (range, 0.4–644.5) m, and there was no statistically significant difference between the sexes.

The majority (67%) of the shelters used by tortoises were burrows dug in soil, followed by pallets (21%) and dens (11.4%). Soil burrows exhibited the following mean dimensions: entrance height, 0.13 m; width, 0.30 m; length, 0.52 m; and angle of declination, 20°. Dens were larger than burrows in most cases, with the following mean dimensions: entrance height, 0.17 m; width, 0.76 m; length, 1.3 m; and angle of declination, 9°. More entrances (56 of 165) faced north (31.5–45°) than in any other direction.

Although 9.1% of inhabited shelters were used by three or more different tortoises, most shelters (73% of burrows and 96% of pallets) were used by a single tortoise during the study. A den was occupied by seven different tortoises in groups of 1 to 4 individuals. Overall, 21 of the 28 tortoises observed shared a shelter with at least one other tortoise. Males shared shelters with an average of 2.6 other males and 1.7 females. Statistically, males and females shared with other males at the same rates; however, males shared shelters with females more often than females shared with other females. Females shared shelters with an average of 2.5 males and 0.5 other females. On average, 35% of the shelters used by an individual were also used by 1 to 6 other tortoises at some point during the study. Females moved among burrows more often than did males in June, during the nesting season; the opposite was observed during the mating season in August and September, when males changed shelters more often than did females (Bulova 1994).

The importance of burrows in the social interactions of Nevada tortoises was studied by Bulova (1997). She tested the responses of tortoises to artificial burrows treated with the feces of an adult male, the feces of an adult female, feces from the subject tortoise, chin gland secretions from an adult male, and untreated burrows, all during both the nesting and the mating seasons. Males spent more time in burrows treated with chin gland secretions than in untreated burrows. During the mating season, significantly more males used the treated burrows. Males were less likely to use burrows treated with the feces of another male. Females were also reluctant to use burrows treated with another female's feces during the nesting season.

During the period from July to October, desert tortoises observed near Las Vegas, Nevada, did not typically sleep in their burrows. Instead, 70% were observed sleeping under bushes. Of those, 86% remained on the surface during the following morning activity period. In contrast, 76% of those tortoises that slept in burrows did not emerge during the following morning activity period (Zimmerman et al. 1994). Sleeping outside in the summer allows tortoises to achieve cooler BTs than they would in a burrow, which may prolong the amount of time they can spend foraging the next morning before reaching a critical BT (Luckenbach 1982).

A large study of burrow use was conducted on the Nevada Test Site near the northern limit of desert tortoise distribution (Rautenstrauch et al. 2002). From January, 1992, to February, 1995, 113 radio-tagged tortoises used 1,558 burrows. Burrows deeper than 1 m (deep) made up 21% of the sample, 70.2% were <1 m (shallow), and 8.8% were of unknown depth (usually because they were blocked by tortoises). Deep burrows were associated with the following natural features: under boulders, 50.8%; under caliche, 25.7%; under shrubs, 13.3%; and in open areas, 9.2%. The remainder were associated with other features. The majority of shallow burrows had the following features: they were under shrubs, 51.4%; under boulders, 26.3%; in the open, 18.5%; under caliche, 2%; or associated with other features of the landscape, 1.8%. Tortoises were found in burrows most often during hot or cold periods. Burrows were used least in April (29% of observations), but burrow use increased to 85% in July, then decreased somewhat in September (69%). Most burrows used during the active season were shallow, but the use of deep burrows increased in October as hibernation began. Males and females used different cover types. Males were more likely to be in deep burrows than were females in all seasons, and they were located deeper in burrows than were females. Tortoises used an average of 11.7 burrows/year, and 90% of the sample used 7–17 burrows/year. Males and females generally used the same number of burrows per year; however, females used more burrows than males in the spring, and males used more burrows than females in the summer and fall. An average of 4.8 new burrows was used each year, and these made up, on average, 39–52% of burrows used annually.

The environmental characteristics of sites selected for burrows by tortoises were studied in an industrial landscape near Palm Springs, California, by Lovich and Daniels (2000). Their study site was characterized by an extensive network of dirt roads, transformers, electrical substations, and other types of infrastructure associated with the construction and maintenance of large windmills used to generate electricity. They collected data to determine whether tortoise burrows were located randomly at the study site and, if burrows were not randomly located, to determine whether tortoises avoid constructing burrows in proximity to human activity and disturbance. Multivariate analysis of the slope, aspect, and elevation of burrows and their distance to various natural and human features in the landscape demonstrated that tortoise burrows were not randomly located and that they tended to be located in proximity to roads and concrete foundations. The authors concluded that tortoises located their burrows near roads because of the "edge-enhancement" effect, whereby runoff from rain accumulates along roads in the desert, often providing a visually conspicuous increase in the biomass of potential tortoise food plants at the edges. A significant number of burrows were located under concrete foundations associated with windmills and transformers. Tortoises may be using this microhabitat for burrow roof stability or for the thermal inertia that large blocks of concrete confer. Concrete may act as artificial caliche, under which tortoises sometimes construct their burrows (Bury et al. 1994, Rautenstrauch et al. 2002).

The characteristics of juvenile tortoise burrows in seminatural enclosures in the Mojave Desert of California were studied by Wilson et al. (1999b). Most burrows were oriented to produce a mean compass direction of 71°, and their orientation differed significantly from a uniform distribution. However, burrows located under shrub canopies had entrances that did not differ from a uniform compass orientation. Burrow dimensions averaged 47.1 cm long and 6.8 cm wide and had an average incline of 8.6° from horizontal. Burrow length and incline were positively correlated with burrow width. Most burrows (80%) were located under shrub canopies (mostly *Larrea tridentata* and *Lycium pallidum*), with 7% under canopy margins and 13% in the open (away from canopies). Large shrubs were preferred over smaller shrubs as burrow locations. Sixteen of 59 (27%) shrubs had two burrows under their canopies, and 1 had three burrows.

Gopherus agassizii is a good climber and often digs its winter den at the top of a steep bank. Woodbury and Hardy (1948) reported that to enter one such den a tortoise had to climb 15.5 m at an angle of about 45°, ascend a vertical gravel ledge 30 cm high at its lowest point, then climb an additional 1.2 m at an angle of about 40°. To enter another den, the tortoise had to climb 40 cm; the first 20 cm led to a narrow ledge just wide enough to accommodate the tortoise's hind feet. Above this, a vertical 25-cm slope led to a 5-cm slope, which in turn led to the entrance to the den. Lovich has observed similarly steep terrain associated with tortoise burrows near Palm Springs, California. A captive female kept by Ernst spent much time attempting to climb walls and pieces of furniture. On several occasions she climbed vertically 15–20 cm up a living room sofa. In accomplishing this she reached up with her forefeet, hooked them under the sofa cushions, and then did a pull-up, raising her hind limbs clear of the floor.

Once in their burrows, desert tortoises resist almost all attempts to remove them. They brace their forefeet against the walls or the floor of the burrow, lean forward, and raise their backs against the roof. This is quite effective, and they are difficult to extract.

Gopherus agassizii is a slow and deliberate animal that often exhibits site fidelity (Freilich et al. 2000). Woodbury and Hardy (1948) measured rates of travel and found that they were 219–483 m/hour. At this speed, it would take 3.3–7.3 hours to travel 1.6 km. The tortoises' velocity ranged from 7.6 cm/second at 25.8°C to 13.5 cm/second at 33.0°C.

In Utah, desert tortoises perform yearly migrations between their winter hibernacula and their summer feeding grounds, where they occupy home ranges that usually cover 4.0–40.5 ha and overlap the ranges of other desert tortoises. There is no evidence that they defend territories in Utah (Woodbury and Hardy 1948) or Nevada (O'Connor et al. 1994b). In California, their home ranges seem more variable. Marlow (*in* Luckenbach 1982) reported home ranges of 10–14 ha, and Vaughan (1983) noted mean home range areas of 7.0 (1.7–34.0) ha for females and 5.5 (0.4–9.5) ha for males. Berry (1986a) suggested that California desert tortoises know the locations of burrows, mates, water sources, and mineral licks within their home ranges, which are 3–89 ha in size. Based on minimum convex polygon estimates, the home ranges of free-ranging tortoises near Las Vegas, Nevada (home range, 5.9–46.0 ha), were not significantly different from those reported by Barrett (1990) for Arizona or by Burge (1977) for southern Nevada. At a translocation site in southern Nevada, males had a mean home range size of 25.5 ha, while that of females was 8.9 ha (Field et al. 2007). It is important to note that minimum convex polygon estimates include areas that are not really used by an animal and areas that may even be unusable. O'Connor et al. (1994b) estimated that an average of 35% of the areas included in minimum convex polygon estimates were not used by desert tortoises. This means that home range sizes may be overestimated substantially in the literature.

Despite the home range areas reported by Vaughan (1983), males may occupy larger ranges than females. Combining their data from southern Nevada with similar data from Burge (1977) for southern Nevada and from Barrett (1990) for Arizona, O'Connor et al. (1994b) found significantly larger home ranges for males than for females but did not find evidence to support the hypothesis that males move more than females during the breeding season. Therefore, there are no data to show that differences in home range size are attributable to reproductive activity, in contrast with predictions for most turtles (Morreale et al. 1984). Freilich et al. (2000) found that the mean minimum convex polygon home range for males at Joshua Tree National Park was 43.5 ha, while for females the mean was 9.7 ha. Their data demonstrate that tortoises travel farther, have larger home ranges, and use more burrows in wet years than in dry years (see also Duda et al. 1999).

Tortoise movements and activities were studied by Duda et al. (1999) at two southern California sites during two dramatically different years. Winter rainfall in 1994–1995 was 225% of the long-term average, while in 1995–1996 it was only 25% of the long-term average for the two sites. During the wet year at one site, the mean home range size for males was 7.7 ha and 7.3 ha for females. During the same year at the second site, mean home range sizes were 26.4 ha for males and 8.5 ha for females. During the dry year at the first site, mean home range sizes were 3.1 ha for males and 0.9 ha for females. During the dry year at the second site, the mean home range size for males was 6.7 ha and for females 1.9 ha. Consistent with the results of Freilich et al. (2000), the average number of burrows used and the average distance traveled between relocations was greater in wet years than in dry years. Also, during wet years tortoises were found aboveground 26% of the time, while in dry years the percentage was only 11%. Reproductive females have larger home ranges than nonreproductive females in Utah, but the difference is not statistically significant (McLuckie and Fridell 2002).

Dispersal of both juveniles (6–8 years old) and neonates (<2 months old) was studied in the central Mojave Desert of California by Hazard and Morafka (2002). The tortoises were headstarted in seminatural nursery pens free of predators, then released outside the pens in mid-October and radio-tracked for at least 34 days. Activity stopped after that time, presumably due to hibernation. The neonates moved uphill, away from the pen in a northwest direction, while the juveniles moved northeast, in the direction of their home hatchery 75 m from the release points. There was no difference in the total distance traveled or in the final linear distance between the two age groups. However, the neonates moved less frequently and entered hibernation locations sooner than did the juveniles. Both groups opportunistically used rodent burrows and adult tortoise burrows as shelters. Neonates and juveniles selected similar burrow microhabitats after being released from seminatural nurseries (Hazard and Morafka 2004). The authors found that while the burrow openings of dispersing neonates were randomly oriented, those of dispersing juveniles tended to face in a mean direction of 162°. Details of the predator-proof field enclosures used are provided by Morafka et al. (1997).

In the west Mojave Desert, neonate and juvenile desert tortoises may be active on winter days, with activity defined as having at least some portion of the body outside the mouth of their burrow. Most of the active juveniles were observed at the mouth or on the mound of their burrow. From 27 November to 23 January, 13 of 71 (18%) turtles observed were active. For 15 days, juveniles were aboveground on six days at 0900 hours, on 10 days at 1100 hours, on 11 days at 1300 hours, and on 8 days at 1500 hours. When temperatures were about 10°C, juveniles were observed outside their burrows during all survey times. At cooler ATs, they were active only during the late afternoon survey. The authors examined relationships between the percentage of active juveniles and vari-ous environmental factors. No correlation was observed with mean or maximum daily ATs (except for the former on the coldest 60 days of the study) or with the amount of rainfall. The minimum daily AT was positively correlated with the percentage of active juveniles (Wilson et al. 1999a).

In Arizona, mean male home ranges vary from 9.2 to 25.8 ha, while those of females vary from 2.6 to 23.2 ha (Averill-Murray et al. 2002a). One Arizona study recorded average home ranges of 19 (3–53) ha for 14 tortoises and found no sexual differences or any correlation with SCL (Barrett 1990). Tortoises used an average of eight burrows each and repeatedly used old burrows. Larger burrows were occupied in the summer; winters were spent in steeper rocky slopes.

Desert tortoises may occasionally move outside of their home ranges. Berry (1986a) reported such movements of 1.4–7.3 km over 16 days to five years. A radio-tagged tortoise in Tucson, Arizona, moved about 15 km in the space of a year, and the total distance it traveled exceeded 30 km (Edwards 2003, Edwards et al. 2004). The great distances reported would not have been possible without human intervention to move the tortoise across an interstate highway, occasional chain link fences, and railroad tracks. During movements, steep drop-offs are avoided (Patterson 1971c).

Gopherus agassizii displays some interesting social relationships. When two tortoises meet, one may nod its head rapidly (head bobbing), and sometimes they touch noses before they pass. When two males meet, a fight is likely to ensue, with head bobbing (although the submissive male may not respond with head bobs) and sniffing followed by biting and ramming (Ruby and Niblick 1994). After the preliminary head bobbing, they separate by a little distance, and then, with heads pulled partway into their shells, rush toward one another. They meet head on and butt their gular projections together violently. Pushing may allow tortoises to assess their rival's BM and thus determine dominance. Fights usually do no damage, but one of the tortoises may be turned over; the vanquished struggles for some time, with one foreleg vibrating vigorously in the air and the other pawing for a foothold on the ground, before he rights himself. If he cannot, he may die of exposure to the sun. A more detailed description of the behaviors involved in male-to-male aggression is provided by Ruby and Niblick (1994).

Interactions between southern Nevada males were studied by Niblick et al. (1994), who placed males individually in 8.3-m^2 pens for one month to establish "residency." Experimental trials involved placing the same pairs of adult male tortoises of various sizes into resident or new pens for 20 minutes and observing their behavior. Three qualities were considered in evaluating the outcome: size, residency, and history of earlier encounters. The results demonstrated that residency and history of earlier encounters played roles in determining dominance. Males that were dominant in their first encounter tended to dominate in the second encounter. In these encounters, neither male was resident, so it appears that size and residency were not factors in the observed outcomes. Larger size was a good predictor of dominance, while residents tended to dominate against same-size challengers. The mean extent of both aggressive and submissive behaviors was greater in novel pens than in resident ones.

Niblick et al. (1994) also examined female choice by placing two males in either a screened or a clear plastic (airtight) box inside the female pen. Males were paired as they had been in the preceding male dominance trials, and female behaviors were recorded for 20 minutes. Each sex showed considerable interest in the opposite sex, and the males were actively head bobbing and following females inside their boxes. Females did not demonstrate a significant preference for larger males in either type of box, nor did they display a significant preference for males scored as dominant. However, when considering only the first exposure of a particular female to a pair of males, females chose the larger male more often. In the authors' final experiment, trios of two males and one female were tested in a pen for about three hours in the morning. Six of eight trials resulted in mounts, always by the dominant male. These males also courted the female more frequently than their subdominant counterpart. In five of the eight trials with mounts, the subdominant male tried to interfere with courtship and copulation. The dominant male then typically stopped courting or mounting and aggressively attacked the subdominant male. Courtship was resumed after the subdominant male retreated.

Campbell and Evans (1967) found that the desert tortoise makes two types of sounds: a short grunt and a drawn-out moan. The fundamental frequency varies by at least an octave (from 0.5 kc to 1.0 kc), and in most cases the signal includes two or three harmonics. These sounds are not involved in courtship or in combat, and their biological significance is not known. Other vocalizations may elicit behavior from nearby tortoises (Patterson 1976). Hisses emitted by startled tortoises or males engaged in aggressive interactions may produce listening or flight behavior. Long calls, if emitted by subordinate males during combat, may bring on feeding or flight responses in dominant males. Pops and "poinks" may also cause flight, and sometimes may cause dominant males to assist overturned subordinate males.

Nichols (1957) reported that after one of her adults drank water it occasionally urinated in its house. Until the house had been thoroughly hosed and aired, other tortoises —one male especially—would not sleep inside unless forced to do so. Patterson (1971b) observed that *G. agassizii* avoided sleeping areas contaminated with fecal matter from other desert tortoises and with urine from male *G. berlandieri.* A captive adult female kept by Ernst, when first introduced to an adult male *G. polyphemus* of about the same size, rammed him several times, causing him to withdraw into his shell. She then walked away and never again showed such aggressiveness toward him during the several years they were kept together; indeed, they were often in each other's company, especially at night. When a small male *G. berlandieri* was introduced to the female, she circled and sniffed him for about a minute and then ignored him.

Ruby et al. (1994b) tested the responses of desert tortoises to various barrier materials designed to keep them from wandering onto roads and being struck by vehicles. Once tortoises encounter a barrier, they tend to continue walking along the perimeter looking for a way through; this tendency to walk along the perimeter decreases somewhat with time. Barriers constructed of small-gauge mesh material with openings too small for a tortoise to insert its head into were considered more effective than solid material because tortoises can see through them, they do not accumulate windblown debris as rapidly, and people can see through them, minimizing unexpected encounters with animals such as venomous snakes. Tortoises are also willing to use culverts under large highways for movements. Fencing projects have been implemented to protect the desert tortoise, reducing tortoise mortality as much as 97% (Boarman 1995, Boarman et al. 1997).

A comprehensive inventory of desert tortoise behaviors observed under both natural and seminatural conditions in southern Nevada is provided by Ruby and Niblick (1994).

REPRODUCTION: There is geographic variation in tortoises' age and size at maturity. Woodbury and Hardy (1948) estimated that in Utah sexual maturity is reached in 15–20 years, when females are 23.0–26.5 cm in SCL and males are 25.0–31.6 cm. In California, Berry (1978) estimated that females first reproduced at 21.5–22.0 cm in SCL at ages of 15–20 years. Turner et al. (1986) reported that females in the Mojave Desert reproduce at 18.9 cm, indicating that they probably mature at between 18.0 and 19.0 cm, although in the northern Mojave of Nevada the smallest reproductive female observed was 20.9 cm and about 19–20 years of age (Mueller et al. 1998). Germano (1994a) reported the following average ages of maturity (in years) for females in various populations: Sonoran Desert, 15.7 years; Sinaloa, 13.8 years; western Mojave Desert, 14.4 years; and eastern Mojave Desert, 15.4 years. The smallest female known to produce eggs in California had a SCL of 17.6 cm (Germano 1994b). The smallest egg-bearing females reported for Arizona were 18.4 cm long, and this size corresponds to an estimated age of 10–20 years, depending on growth conditions in the area (Averill-Murray and Klug 1999, Averill-Murray et al. 2002b). Miller (1955) reported that male secondary sexual characteristics begin to appear at 16 years, are definite at 17 years, and are complete at 20 years of age. One of our captive females 16.5 cm in SCL (10–11 years old) stimulated courting activity in a large male. Tortoises kept in captivity on an enriched diet and active all year grow faster and may reach a mature size in much less time than do those in the wild, 12–13 years (Stewart, *in* Berry 1978), but possibly as little as 4 years (Jackson et al. 1976, 1978).

Juvenile *Gopherus agassizii* (C. H. Ernst)

The sexual cycle of southern Nevada males was described by Rostal et al. (1994a) and by Lance and Rostal (2002). The seminiferous tubules are completely regressed in April, containing only spermatagonia and Sertoli cells. At this time, the Leydig cells are greatly hypertrophied, filling the interstitial area. By July, spermatocytes and spermatids are numerous, and a few mature spermatozoa are present. Spermatogenesis reaches a peak in October, before hibernation; the seminiferous tubules are at their maximum diameter, and the Leydig cells remain in their hypertrophied condition. After the tortoises emerge from hibernation in April, the lumens of the seminiferous tubules are filled with cellular debris from the previous cycle, and large numbers of spermatogonia and spermatocytes are still present. At this time, the Leydig cells are not well developed and not present in abundance. The levels of plasma testosterone are low in April and part of May, then rise significantly from May to August, remaining high through the fall mating period. These levels range from a mean high of 243.6 mg/mL during the fall mating period to a mean low of 18.37 mg/mL during May, when nesting begins in this population. Corticosterone levels peak in July–October and are higher in males than in females at all times of the year (Lance et al. 2001). The highest levels in males are associated with peak spermatogenesis and male-male combat. From June to September, males' BM also increases significantly. Just prior to hibernation, their plasma testosterone levels decline. Their testosterone levels remain low during the spring mating season after emergence from hibernation. Testosterone levels may rise in response to interactions with other tortoises when males are attempting to establish territories, and they also rise with ATs from June to August.

Free fatty acids are the only plasma lipids that occur in higher levels in males than in females during the period from April to October. Total concentrations of plasma lipids, including free fatty acids and cholesterol esters, decrease in males with an increase in testosterone and the occurrence of spermatogenesis. These results suggest an association between testicular development and lipid metabolism (Lance et al. 2002). Plasma thyroxine peaks in reproductively active males during July (Kohel et al. 2001).

The volume of male chin glands varies seasonally, along with the level of plasma testosterone, reaching a maximum in late summer (July–August). Socially dominant males tend to have larger chin glands than do socially subordinate males. Experiments with empty lacquered desert tortoise shells with chin gland secretions applied to the gular scute demonstrated that desert tortoises of both sexes could discriminate between the odors of familiar and unfamiliar males. This suggests that chin gland secretions may play an important role in recognition among tortoises. Molecular studies of the secretions identified 12–17 protein components ranging in size from 25,000 to 115,000 Daltons (a unit of atomic or molecular mass), as well as several types of lipids, including volatile free fatty acids. There are slight individual differences in the chemistry of gland secretions among male *Gopherus*, further adding to the potential for these secretions to perform a recognition role, possibly at the individual level (Alberts et al. 1994, Rose et al. 1969).

The female sexual cycle was described by Lance and Rostal (2002), Lance et al. (2002), and Rostal et al. (1994a). After the completion of nesting season, vitellogenesis and ovarian follicular development occur (July–October), coincident with peak ATs. Vitellogenesis is induced by the hormone estradiol, which also regulates the total lipid concentrations in plasma. Prior to hibernation, the ovarian follicles mature to a mean ovulatory size of 2.43 cm. Shelled eggs are first observed in the oviducts in mid-April. Ovulation occurred in 90% of the females by 30 April, and eggs were in the process of being shelled. Following nesting, atretic follicles were often observed that were smaller (0.7–1.9 cm) than preovulatory vitellogenic follicles. The walls of the ovarian follicles are separated into two components, an outer layer and an inner layer; the inner layer responds to gonadotropin stimulation by producing progesterone (Crews and Licht 1975).

Female testosterone levels rise significantly prior to hibernation and coincident with fall mating (July–October). These levels go even higher following emergence from hibernation and prior to ovulation in April and May (6.22 ng/mL). Female testosterone reaches a mean low of 0.37 ng/mL during the late nesting period in July. The levels of plasma estradiol, corticosterone, and lipids are elevated in April, and the levels of estradiol and lipids associated with vitellogenesis are higher in August, September, October, and April than they are in June. Progesterone levels increase in April and May, then rapidly return to baseline levels after the eggs are laid. Most hormones and lipids decline to low levels in May and June except for thyroxine, which is at its lowest levels in October and during hibernation (Kohel et al. 2001).

Female corticosterone levels have a definite peak in May but are always significantly lower than in males (Lance et al. 2001). Plasma calcium levels also vary seasonally for females and are significantly elevated in the fall (July–September), along with the levels of plasma lipids and estradiol, during follicular growth and vitellogenesis. These levels ranged from a low of 8.2 mg/dL in April, after emergence from hibernation, to a high of 16.38 mg/dL in August, at the end of the nesting season. Male levels were low in the fall, increased from April to May, then remained fairly constant from May to September. The white cell counts of both sexes were low from April to June and elevated from August to October. Females' BM changes seasonally and is lowest during the spring nesting season and the fall vitellogenic period.

The oviducts of females contain tubules capable of supporting viable sperm for some time, so sperm from one mating may be used to fertilize several clutches of eggs (Gist and Jones 1989, Palmer et al. 1998). There is no evidence of reduced fertility of clutches based on storage time. The mean hatching success of clutches studied in Nevada was 95.8%. For clutches produced with sperm stored by the female for over two years, hatching success was 97.1%. Sperm storage may be an adaptation to compensate for the lack of complete synchronization between male and female sexual cycles or to ensure a supply of sperm to fertilize first and subsequent clutches (Pearse and Avise 2001). There is tentative evidence of multiple paternity in which a single clutch contains eggs fertilized by more than one male (Palmer et al. 1998).

Courtship and mating begin shortly after spring emergence, possibly as early as 25 March, and continue through the summer and into the fall, as late as October (Luckenbach 1982, Medica et al. 1982, Tomko 1972). Rostal et al. (1994a) reported two periods of mating and male combat activity in southern Nevada: April–May and August–November. At another Nevada location, most courtship was observed in the fall (Rautenstrauch et al. 1998).

Black (1976) and Weaver (1970) indicated that courtship begins with the male approaching the female. If she remains motionless or bobs her head at the male, he may touch parts of her shell and head, perhaps to verify her sex through olfactory cues. Male head bobbing may also occur at this stage. However, if the female crawls away, the male will trail her with low-intensity head bobs and his neck not fully extended. The intensity of head bobbing increases as the female speeds up her walking, and the male now stretches his neck to the fullest extent. When the female is caught, he continues high-intensity head bobbing while circling her (usually in a counterclockwise direction). She usually tries to move on or circles him. Once she stops, the male reduces the frequency of head bobbing and starts to bite her nose, forelegs, and shell. She usually pulls in at this stage, and she may continue to circle to avoid the male. He rams her with his gular projection, and she finally ceases to move. When males ram females, it is usually a much less violent action than in male-male interactions (Ruby and Niblick 1994). Some males court in front of female burrows, bobbing their heads in the direction of the female (Bulova 1994).

After courting, the male attempts to mount the female from the rear or side, assuming a nearly erect position, with his forelimbs resting on her carapace. He then performs vertical pumping movements, accompanied by puffing and grunting noises. Most reports of vocalization during breeding activities suggest that the sounds are a by-product of the copulatory effort; nothing indicates that they serve as an auditory signal (Weaver 1970). Females may signal a successful copulation by fully extending their necks, then retracting them (Niblick et al. 1994). Nichols (1953) reported that each spring a captive male chose a mate for the season —usually a different female from that chosen the previous year. Nichols (1957) reported a female initiating courtship.

Several of the complete courtships observed by Black (1976) lasted more than 80 minutes. Additional details on courtship and mating sequences are provided by Ruby and Niblick (1994).

The nesting season extends from mid-April into August. In California, larger females produce eggs earlier in the season than do smaller females (Wallis et al. 1999). In Arizona, the timing of egg laying occurs before or near the onset of the beginning of the summer monsoon rains (Averill-Murray 2000b, Averill-Murray et al. 2002b, Murray et al. 1996), a possible adaptation to avoid intense rainfall (Van Devender 2002b). In Arizona, the average egg-laying date does not appear to be related to recent rainfall, based on three years of data summarized by Averill-Murray et al. (2002b). Females have been known to lay eggs as late as September–October and to nest 2–3 times in one season (Luckenbach 1982).

Early morning and late afternoon seem to be the favorite nesting times. The eggs normally are deposited in cavities dug in sandy or friable soil but are also laid in the mouths of burrows or under vegetation (Murray et al. 1996, Rostal et al. 1994a). Hampton (1981) found that most nests in the Fremont Valley, Kern County, California, were located at the entrance of a large burrow; 12 of 15 were located in the shade of a creosote bush because of the burrow's location, while only 3 were in the open.

In the days just prior to nesting, the female often becomes extremely restless and spends considerable time scratching the soil with her forefeet. She may refuse to eat during this period. After oviposition, females spend less time aboveground than do males (Luckenbach 1982). Males remain aboveground longer than females and apparently continue sexual activity throughout the summer, as females become available. Of 124 tortoises examined in the field by Luckenbach (1982) in August 1973, 80% were adult males.

The nest cavity is usually dug by the hind feet, but the area may first be cleared and the initial scraping done by the forefeet (Luckenbach 1982). In Arizona, nests are constructed in sandy soils (Murray et al. 1996). The hind feet are used to dig the nest, to arrange the eggs in the nest, and to scratch and drag soil back into the cavity after the eggs are laid. The female may release bladder water into the nest cavity before filling it or on it after filling it. The water may soften the soil for digging, repulse egg predators, camouflage the nest cavity, and compact the soil over the finished nest to make nest excavation by predators difficult (Patterson 1971a). Bjurlin and Bissonette (2004) observed female tortoises voiding water on 12–25% of the nests observed during two years of study, but the presence or absence of water did not affect nest survival. Excavation of the nest may take one hour to several hours, oviposition 15–30 minutes. The nest is funnel-shaped (wider at the entrance than in the egg chamber). The depth is 8–25 cm. Nichols (1953) gave the measurements of a typical nest as approximately 15 cm deep, 23 cm diameter at the top, and 18 cm across at the bottom. The nests of captives listed by Hampton (1981) varied from 10 to 20 cm in diameter and from 10 to 25 cm in depth.

Clutches consist of 1–15 eggs; about 4–7 is the usual number. In the Sonoran Desert of Arizona, where females lay only one clutch/year, the clutch size ranges from 1 to 12 (Averill-Murray et al. 2002b), with 0.78 clutches/female at one Arizona site (Murray et al. 1996). Clutch size (California, Wallis et al. 1999), clutch frequency, and annual egg output (Utah, McLuckie and Fridell 2002) may be directly correlated to the SCLs of females in some areas but not in others (Arizona, Averill-Murray 2002a), and 1–3 clutches may be laid each year, depending on geographic location and food availability. In Nevada, clutch size and annual egg output are correlated with the female's SCL, but clutch frequency is not (Mueller et al. 1998). Annual egg output varies more as a function of clutch size than of clutch frequency (Wallis et al. 1999). Near Palm Springs, California, the mean clutch size of the second clutch was larger than the mean for the first clutch in one year, 4.3 and 5.0 eggs, respectively, and a female deposited a third clutch of 3 eggs that same year (Lovich et al. 1999). In contrast, in southern Nevada the mean clutch sizes were 5.1 and 3.7 eggs for the first two clutches, respectively (Rostal et al. 1994a), the reverse of what was observed in Palm Springs. These differences likely represent differences in resource availability for tortoises between the two studies. In Utah, the mean size of both the first and second clutches was 5.2 eggs (McLuckie and Fridell 2002).

The eggs of *G. agassizii* vary from elliptical to nearly spherical in shape. The dimensions of four eggs measured by Miller (1932) are representative for the species (see also Luckenbach 1982, McLuckie and Fridell 2002, Wallis et al. 1999) and had the following dimensions: length, 4.16–4.87 cm; maximum width, 3.67–3.96 cm; and minimum width, 3.49–3.82 cm. Egg size can vary geographically; females produce smaller eggs in the east Mojave Desert (mean, 4.09 cm), where both winter and summer rains fall in some years, than in the west Mojave Desert (mean, 4.52–4.55 cm in two years), where very little summer precipitation falls. It is possible that the more predictable environment created by biphasic rainfall relaxes the need for larger hatchlings that can survive the harsher conditions created by winter rainfall alone (Wallis et al. 1999). After removing the effect of female SCL, larger clutches contain smaller eggs, and tortoises that lay only one clutch a year produce smaller eggs than those that oviposit twice (Wallis et al. 1999). Fresh eggs weigh 33–34 g (Luckenbach 1982) and are moist, translucent, and extremely hard, with a coarse, rough texture and without gloss, a chalky layer, or pigment. The translucence, which permits observation of a small gas bubble within the egg, disappears upon drying. The gas bubble remains for several months without change in volume, an indication that the shell is moisture-proof. Egg width, but not egg length, was correlated with female SCL in a Utah population (McLuckie and Fridell 2002). In Arizona, mean egg width is not related to year, amount of rainfall, or clutch size (Averill-Murray 2002a). At Twentynine Palms, California, relative egg volume is not correlated with female SCL (Bjurlin and Bissonette 2004). Egg yolks contain 90% of the nitrogen in the eggs, and females invest up to 85 mL of water in egg production (Henen 2002a).

The reproductive output of *G. agassizii* is strongly related to the productivity of annual food plants in the desert (but see Turner et al. 1986), which in turn is related to the timing and amount of precipitation (Averill-Murray and Klug 1999). El Niño events can trigger spectacular germination in the desert (Oftedal 2002), producing an abundance of food plants. Berry (1978) reported that it is possible that females do not lay eggs in years when forage production is low, and Averill-Murray et al. (2002b) presented Arizona data in support of this hypothesis. In the latter study, clutch size appeared to be smaller in years with less rainfall, and a smaller proportion of mature females, especially small ones, produced clutches in times preceded by low rainfall (Averill-Murray 2002a). California females respond a little differently to resource availability. Lovich et al. (1999) observed that the mean clutch size was relatively constant during both El Niño and drought conditions. However, the proportion of reproducing females and the number of clutches produced (1–3) were both positively correlated with the amount of precipitation and forage productivity.

Because tortoises are selective foragers, the level of annual plant productivity may be a poor indicator of the abundance of preferred food species or the availability of specific nutrients (Henen 2002a). Therefore, the nutrients and energy used by females to produce eggs come not only from spring food plants but also from energy stores in their bodies. Henen (2002b, 2004) referred to these resources as "income" versus "capital," respectively, and concluded that females use both forms of energy for reproduction. Henen (2002a) concluded that the allocation of nonlipid material to eggs accounted for 37% of the observed declines in the nonlipid matter of female bodies. He further concluded that nonlipid matter, likely nitrogen from protein harvested prior to hibernation, but not energy itself, limits egg production in *G. agassizii*. Total female reproductive output is highly correlated with the amount of nitrogen consumed the preceding year. The total amounts of body energy, nonbody energy, and body water are higher in nonreproductive females than in reproductive females, as would be expected (Henen 2002a). Water and protein appear to be important limiting factors of reproduction in drought years.

Even in drought years, some female tortoises continue to produce eggs by relaxing their control of energy and water homeostasis. Energy does not limit egg production directly, but it is likely that protein and water availability are limiting factors. As expected, females that forgo opportunities to reproduce in dry years store more body nonlipid energy and lose less body water than those that do. In fact, females' reproductive effort (measured as the amount of energy allocated to reproduction divided by the amount of energy needed for all vital expenditures) is greater during a drought year than during a wet year, because females have the ability to reduce their field metabolic rates 70–90% during a drought. The strategy of sacrificing the condition of their bodies to produce a few eggs is consistent with a life history strategy called bet hedging. Under this strategy, tortoises do not skip opportunities to reproduce under poor conditions but rather continue to try to produce some eggs every year (Henen 1997, 2002b).

Not all mature females reproduce in a given year; reproduction depends on environmental conditions and resource availability. In 1997 and 1998, Lovich et al. (1999) simultaneously studied the reproductive output of radio-tagged tortoises at three locations in California using x-ray photography. All sites were recovering from drought in 1997, but 1998 was an El Niño year with significant rainfall. In 1997, 9 of 10 females near Palm Springs, California, reproduced; 6 of those deposited double clutches, and 1 deposited a third clutch. Nearby, Joshua Tree National Park was experiencing a severe drought, and there only 1 of 8 females reproduced. In Mojave National Preserve, conditions were intermediate, and 12 of 18 females produced one clutch each. After the El Niño conditions in 1998, 12 of 13 tortoises at Palm Springs reproduced; all laid a second clutch, and almost 33% produced a third clutch. The mean first and second clutch sizes did not differ between 1997 and 1998 at this site. At Joshua Tree National Park, 100% of the females laid eggs, and 71% produced a second clutch.

The mean annual clutch frequencies of California females for 1983–1985, as determined by x-rays, were 1.6–1.9 clutches (Turner et al. 1986). The tortoises typically laid 1–2 clutches during May and June, but one female did not oviposit in 1984, and single tortoises laid 3 clutches in 1983 and 1985. If females laid 2 clutches, the second was faintly visible in x-rays within 9–10 days after the first was laid. Eggs were laid about 22 days after they were first visible in x-rays. Usually it was the larger females that laid multiple clutches. Clutch sizes were positively correlated with female SCL, but when this effect was removed, clutch sizes did not differ between years, the first and second clutches laid in a season did not differ in size, females laying only 1 clutch laid larger clutches than females laying more than 1 clutch per season (as they do in Nevada according to Mueller et al. [1998] but not in the results reported from California by Wallis et al. [1999] unless the effect of body size is removed), and the variation in clutch sizes of different individuals was greater than comparable variation for the same tortoises. Mean clutch frequencies were positively correlated with winter rainfall, but summer rains also apparently contributed to the reproductive energetics of the females. Adult females in California had two periods of distinct weight loss in 1980 (15–28 May, 12–25 June), which Turner et al. (1984) interpreted as evidence of egg laying.

In Utah, the mean clutch frequency was 1.33 clutches / reproductive female, resulting in an annual egg output of 3–18 eggs among females (McLuckie and Fridell 2002). The mean clutch frequency in Arizona was 0.78 clutches/female (Murray et al. 1996). The annual egg output in Nevada ranged from 0 to 16 eggs and was predicted to be 3 eggs for a female 20.8 cm in SCL, increasing by 1 egg for each 7 mm increase in SCL thereafter (Mueller et al. 1998). Comparing the data of Mueller et al. (1998) with those of Turner et al. (1986) showed that the annual fecundity of California females averaged 4.5 eggs more than that of Nevada females, despite the fact that the California females were smaller (mean SCL, 21.1 cm) than the Nevada animals (mean SCL, 24.7 cm).

Hatching occurs from mid-August to October, with peak emergence in September and early October. Natural IPs usually last 90–120 days, but artificially incubated eggs hatch in 82–92 days. The mean IP varies with IT as follows (Lewis-Winokur and Winokur 1995): 25°C, 124.7 days; 27°C, 103.8 days; 28°C, 87.1 days; 29°C, 84.2 days; and 31°C, 78.2 days. In captivity, a hatching rate of 89% is considered high; normally the rate is about 60% (Luckenbach 1982). Turner et al. (1986) reported that only 26 of 57 (46%) eggs moved to predator-proof nests in May and June hatched by the end of October; however, none of the 17 apparently viable eggs left in the protected nests until 3 May hatched. Excluding eggs destroyed by predators, Bjurlin and Bissonette (2004) observed hatching successes of 81.6 and 83% during two years of study at Twentynine Palms, California. Of 26 nests examined, 61.5% had total egg hatching success. However, only 50% of nests had total hatchling emergence, because some young tortoises were entombed. Nests that experienced partial hatching success (30.8%) generally produced at least 1 emergent hatchling, but some (8%) produced none. While hatching success was not correlated with female SCL, after removing the effect of relative egg volume, females larger than 24.0 cm had increased hatching success and neonate emergence success relative to those smaller than this.

Emergence may be asynchronous and span at least 15 days (Averill-Murray et al. 2002a). At Twentynine Palms, California, siblings emerged more or less synchronously. The percentage of nests that completed emergence in the following time intervals were 1 day, 8.7%; 2 days, 30.4%; 5 days, 17.4%; or 7 days, 13%. Those hatchlings that took a long time to emerge were generally abnormal in some way, and their nests took longer for complete emergence than nests without deformed hatchlings (Bjurlin and Bissonette 2004). Grant (1936) reported a case of overwintering in the egg, with hatching the following spring, and Averill-Murray et al. (2002a) suggest that overwintering might occur in Arizona.

Hatchlings are nearly as wide as they are long and are 3.6–4.9 cm in SCL, 3.2–4.3 cm in CW, and 1.9–2.9 cm in CH. Their carapace varies from dull yellow to brownish, with darker brown areas on each of the scutes. The color and shape of the hatchlings are such as to render them practically invisible among stones and dry grasses. The shell is pliable, and there are wrinkles on the sides and a deep crease across the plastron that allowed curling of the fetus in the egg. In the center of the plastron is a yolk sac about one-third the size of the young turtle; the sac greatly impedes its movements. This is rapidly resorbed over a two-day period, leaving only a soft umbilical scar by the third day; it remains visible for several weeks and does not completely heal for several months. The caruncle disappears gradually. The cervical and the twelfth marginals are incomplete at hatching and are deeply notched and bluntly serrate on the rim. As Morafka (1994) noted, the eggs of North American tortoises like the desert tortoise are about 350% of the mass of eggs of their sister taxa in the Emydidae and produce hatchlings with about twice the mass of aquatic emydids. The large size of tortoise eggs and hatchlings may be an adaptation to the harsh and unpredictable environment of the desert tortoise in comparison with the habitats of most emydids. Hatchlings' size is related to incubation conditions and positively correlated with egg mass, even after 120 days. Hatchlings produced at ITs of 32.8 and 35.3°C are significantly smaller than hatchlings incubated at 28.1 and 30.6°C (J. R. Spotila et al. 1994).

Lance et al. (2002) found that the major lipid components of yolk included triacylglycerol, phospholipids, and cholesterol. The yolk of hatchling desert tortoises contained the following means (μg/mL) and percentages of lipids: triacylglycerol, 77,436 (79%); phospholipids, 16,018 (16%); cholesterol, 2,229 (2.3%); cholesterol ester, 2,281 (2.3%); and free fatty acid, 204 (0.002%). The total lipid concentration was 98,054 μg/mL. These percentages roughly mirror those of female plasma lipid concentrations during vitellogenesis in August–April in that triacylglycerol and phospholipids make up the majority of the components. The principal lipid components of hatchlings' plasma are cholesterol ester followed by phospholipids, with triacylglycerol making up only 9.4% of the total lipids. The lipid concentrations were higher in fasted hatchlings than in fed ones, suggesting that the metabolism rate of fed hatchlings is higher and that they absorb yolk faster. The large yolk reserve of hatchling tortoises likely allows them to disperse and survive emergence in the Mojave Desert when conditions are not favorable for food plants and feeding (Lance and Morafka 2001). However, winter feeding has been observed in neonate and juvenile desert tortoises in the west Mojave Desert (Wilson et al. 1999a).

The desert tortoise has TSD-1a, with a pivotal temperature of about 31.3–31.8°C (Lewis-Winokur and Winokur 1995, Rostal et al. 2002, J. R. Spotila et al. 1994). The relatively high pivotal temperature may be a response to the warm climate that modern desert tortoises occupy. Rostal et al. (2002) reported that at ITs of about 30.5°C or less, only males are produced. Temperatures of 32.5°C or above produce 100% females. J. R. Spotila et al. (1994) found that low ITs of 26.0–30.6°C produce males, while females are produced at temperatures of 32.8–35.3°C. The results of Lewis-Winokur and Winokur (1995) were somewhat different in that they reported a sex ratio of males to females of 5:7 at an IT of 31°C, while ITs of 25, 27, 28, 29, and 29.4°C produced only males. The difference between their results and those of other authors may be due to the fact that the former used the eggs of captive tortoises that were removed from the nest up to 16 days after oviposition before being transferred into the laboratory. Hatching success was low at low ITs (excluding potentially infertile clutches): 25°C, 53%; 27°C, 89%; 28°C, 83%; 29°C, 100%; and 31°C, 85%. ITs also affected hatchlings' survival, measured as those living 277 days or longer: 25°C, 20%; 27° C, 33%; 28°C, 81%; 29°C, 88%; and 31°C, 72%. Egg fertility can be determined from the presence of an opaque white spot on the egg where the embryo attaches (Lance and Morafka 2001).

ITs continue to affect shell morphology and thermoregulatory behavior well after hatching. Hatchling tortoises from throughout Las Vegas Valley were randomly assigned to three environmental chambers with different temperatures (19, 28, or 37°C) for four months, then transferred to a common 28°C holding facility. Daylight cycles (12D:12N) and feeding regimens were similar among treatments. At nine months of age, thermocouples were placed on the hatchlings' shells and inserted into their cloacas before they were placed in another chamber where they could freely thermoregulate along a thermal gradient ranging from 23 to 45°C. Hatchlings held at 28°C increased their BMs at a higher rate than those held at either of the other two temperatures. After transfer to the 28°C common holding facility, growth rates were similar among the groups. One week after hatching, all tortoises had similar mean SCLs, CWs, and CHs, but after four months those held at 37°C were flatter and had greater ratios of surface area to volume (mean, 0.82 cm^2/mL). In comparison, those held at 19 and 28°C were rounder and had lower ratios of surface to volume (means, 0.61 and 0.74 cm^2/mL, respectively). Tortoises from the 19 and 28°C treatments had lower BTs and cycled between temperatures in the gradient more often than those kept at 37°C (Reiber et al. 1999).

Hatchlings' sex is determined as early as embryonic stage 15 or before and as late as stage 21, depending on the IT. Differentiated gonads are histologically detectable between stages 18 and 21 and are obvious by stage 23. From the time desert tortoises hatch until they are about three months old, they have incomplete and poorly developed seminiferous tubules. After six months, seminiferous tubules are clearly visible in males, while females show prominent Müllerian ducts and yolk-laden ovarian follicles (Lewis-Winokur and Winokur 1995). Optimal incubation conditions occur on dry sand between 28.1 and 32.8°C. Incubation at the high end of these temperatures is lethal to 72% of the eggs, and hatchlings that do emerge die within 45 days. Similarly, wet sand has lethal effects: no eggs incubated at 26.0°C and 4% soil moisture hatch (J. R. Spotila et al. 1994).

GROWTH AND LONGEVITY: Germano (1994a) observed that the largest *Gopherus* species, *G. flavomarginatus,* grows at the fastest rate, while the smallest species, *G. berlandieri,* grows at the slowest rate. It is not surprising that *G. agassizii,* intermediate in size between those two congeners, has growth rates that are intermediate. The species' annual natural feeding period may last only 6–12 weeks in good forage years, which occur, on average, once every five years (Luckenbach 1982). Lean years may delay growth and maturation, because both are apparently enhanced by greater food availability and quality in captives (Jackson et al. 1976, 1978). The juvenile shell remains soft for 5–10 years. Hatchlings' growth is related to ITs. Those produced from eggs incubated at 30.6°C grow faster than those from eggs incubated at 28.1 and 32.8°C (J. R. Spotila et al. 1994). Many data have been published on the growth rates of captive *G. agassizii* (Jackson et al. 1976, 1978; Miller 1932, 1955; Patterson 1977, 1978; Patterson and Brattstrom 1972).

Bogert (1937) reported that a wild female grew 2.2 cm in 680 days and that a smaller one grew 7.0 cm in 818 days. Woodbury and Hardy (1948) found that many young *G. agassizii* grew to a SCL of about 10.0 cm in five years. The most rapid growth they recorded was that of a tortoise that grew from 20.6 to 30.2 cm in little more than 52 months. Growth is more rapid up to about 18 years and then slows in larger tortoises (Germano 1994a).

Natural growth and age-size relationships in tortoises from Nevada were studied by Medica et al. (1975) and Turner et al. (1987). Growth was affected by variations in rainfall, which controlled plant growth. The tortoises' average annual growth between 1963 and 1973 was about 9 (1.8–12.3) mm, and this generally occurred between April and June. None of the animals measured during this period was mature, and they had original PLs of 4.7–7.4 cm. By 1985, all of the tortoises were at least 20 years old. Over this period, the growth of males and females did not differ significantly. Tortoises reached PLs of 10 cm in 6–7 years, 13 cm in 10–11 years, and 15 cm in 13–14 years, and they measured more than 20 cm at estimated ages of 24 years. Germano (1994a) found that the mean width of annual growth rings was negatively correlated with mean annual precipitation, a surprising relationship.

The use of scute annuli to age tortoises is controversial (Wilson et al. 2003). According to Germano (1988), scute annuli produced during the first 20–25 years of initial growth can be used to age tortoises, but for most tortoises annuli counts reflect one or two rings fewer than the animals' actual years of age. In contrast, Tracy and Tracy (1995) observed from 0 to 14 growth rings on laboratory-reared tortoises that were 1–2 years old. The number of growth rings thus averaged 0–7/year. The number of scute rings was correlated with PL, not age. Although these results are intriguing, they do not mirror those shown in wild or captive tortoises kept under seminatural conditions (Germano 1998). Probably the results reported by Tracy and Tracy are artifacts of the artificial conditions (constant laboratory conditions and a high-protein diet) under which the subject tortoises were housed and fed.

Berry (2002) examined growth rings from 11 tortoise populations in the Mojave and Colorado Deserts of California and found that 0 to ≥3 rings were formed annually. The subannular rings could not be visibly distinguished from the annual rings. The mean number of annual rings varied from 0.86/year in the western Mojave Desert to 1.17/year in the northeastern Mojave Desert. The annual production of rings also varied among years at Goffs, California, and was positively correlated with total, winter, and summer precipitation. Weak positive correlations were detected between ring counts and the biomass of annual herbs and the exotic grass *Schismus* sp. and also between ring counts and annual herbs only. Germano (1998) used data from captive and wild tortoises to demonstrate that hatchlings and one- and seven-year-old juveniles had exactly the same number of annuli as their years of age but that the number was generally one less than the age by the time the tortoises were 15–20 years of age. His results suggest that growth annuli are accurate measures of age in young tortoises as long as the rings are counted by experienced observers.

Germano (1992) found that the growth rates of tortoises varied between populations, with the most growth (0–25 years) occurring in tortoises from the western Mojave and Sinaloan Deserts and the least growth in the eastern Mojave and Sonoran Deserts. At age 1, tortoises from the western Mojave and Sinaloan Deserts have average SCLs of 5.1 and 5.9 cm, respectively, while those from the eastern Mojave and Sonoran deserts are only 4.6 and 4.9 cm, respectively. At age 10 years, tortoises from the eastern Mojave and Sonoran populations have grown to an average of only 12.2 and 12.5 cm; their growth is surpassed by that of the western Mojave and Sinaloan tortoises (14.0 and 13.9 cm, respectively). By age 20, *G. agassizii* from the eastern Mojave average 20.7 cm in SCL and those from the Sonoran Desert 21.1 cm; desert tortoises from the western Mojave population are 23.9 cm long and those from the Sinaloan Desert 21.1 cm in length.

In Arizona, *G. agassizii* reach 36–47% of their maximum SCL before their growth rate begins to slow. Males reach larger average sizes than females at all sites surveyed north of the Gila River. South of the Gila River, females reach sizes similar to or larger than those of males (Averill-Murray et al. 2002b). The reasons for these differences are unknown, but sampling bias needs to be examined carefully in such studies.

Many wild adult *G. agassizii* are between 20 and 30 years of age, but, based on minimum estimates of longevity, it appears that few live 50 years. Maximum longevity estimates for Sonoran Desert tortoises (based on growth equations for size and age at SCLs within 0.1 mm of asymptotic size) are 62.2 and 64.4 years for females and males, respectively (Germano et al. 2002). Approximately 29% of the desert tortoises from the Sonoran Desert, 11% of those from the eastern Mojave Desert, and 5% of the tortoises from the western Mojave Desert survive <25 years (Germano 1992). The oldest individual from the western Mojave Desert was estimated to be 32 years old, the oldest from the Sonoran Desert 35 years old (Germano 1992). However, some captives have been very long-lived. Nichols (1953, 1957) reported that a male *G. agassizii* captured in 1929, when 4 or 5 years old, was still alive when 32 or 33 years old, and Patterson and Brattstrom (1972) also reported individuals older than 30 years. Snider and Bowler (1992) reported that one lived 55 years, 1 month, and 30 days in captivity. Jennings (1981) reported a male potentially 67–72 years old, and Glenn (1983) noted a female that may have been alive for 80+ years and was possibly a centenarian when she died.

DIET AND FEEDING BEHAVIOR: *Gopherus agassizii* is normally an obligate herbivore, subsisting largely on various annual and perennial forbs, grasses, cacti, and other nonwoody plants. The four species of *Gopherus* have an os transiliens, a small sesamoid bone in the central raphe of the external adductor muscle found in no other Recent tortoises (Bramble 1974a, Patterson 1973a), which seems to be an adaptation for feeding on coarse xerophytic vegetation, with the exception of sclerophyllous plants (with hard leaves) so typical of many desert perennial plant species (Morafka and Berry 2002). Tortoises are capable of eating large amounts of food when it is available. Laboratory tests using grass and high-fiber pellet diets indicate the contents of a tortoise's digestive tract can make up 11–21% of its BM, about 13% in the wild.

The desert tortoise's digestive system is adapted to a diet high in abrasive materials, including fibers and spines (Barboza 1995a). There are considerable differences in the gut layers and gut morphology between adult tortoises and juvenile and hatchling tortoises, likely a reflection of the differences in diet between the two broad age classes (Winokur et al. 1998). The mucosal layer of the esophagus has elongated, sometimes branching, papillae in juveniles but not in adults. Adults also have a well-developed muscularis mucosa in the esophagus; juveniles have a thin and single-layered equivalent. In their stomachs, juveniles possess numerous tubular acinar glands in contrast to the elaborate branched villilike projections seen in adult stomachs. The distal portion of the duodenum has long, broad papillae, but the density of these papillae is greater in juveniles. The percentages of the lengths of the various parts of the digestive tracts of hatchling and juvenile tortoises are as follows: esophagus, 7.4%; stomach, 15.3%; small intestine, 28.3%; and large intestine, 48.2%.

Like other vertebrate herbivores, *G. agassizii* are incapable of producing the enzymes necessary to digest cellulose, so they presumably cannot digest woody materials (Oftedal 2002). These enzymes are produced for tortoises by gut microorganisms (including the potentially dangerous bacterium *Clostridium bifermentans;* Dezfulian et al. 1994) that they first obtain as juveniles through copraphagy (Lance and Morafka 2001, Morafka et al. 2000). Desert tortoises have also been seen eating the feces of black-tailed jackrabbits (*Lepus californicus*), and this behavior either provides them with nutrients or allows for interspecific transfer and inoculation of symbiotic gut microbes as in juveniles (Walde et al. 2006). Murray (1997) observed one tortoise eating a raptor pellet, possibly as a source of minerals from the bones contained in the pellet. The colon is the main location of microbial fermentation. Digestion of fiber contributes 64% of the digestible energy in grass (Barboza 1995a).

Desert tortoises may prefer annual plants (Henen 2002a) because of their high spring protein concentrations, relatively high water content, or high PEP indexes (see Behavior). On occasion, tortoises eat nonplant material, but that is exceptional. Lists of plants eaten by wild desert tortoises are presented in Burge and Bradley (1976), Hansen et al. (1976), Luckenbach (1982), Oftedal (2002), and Van Devender et al. (2002). The most important foods seem to be desert annuals, plants that often have a life span of less than 30 days and are generally available only from April to June. Preferred plants are often uncommon or rare in tortoise environments (Jennings 1997).

Both flowers and vegetative parts of plants are eaten, but when available, flowers are preferred (Ernst, personal observation; Luckenbach 1982), and peak tortoise activity corresponds to the period of spring blooming in the western portion of the range and to the summer monsoons in the eastern part of the range (Averill-Murray et al. 2002a). Because food quality decreases dramatically after June, tortoises must eat enough to carry them through both summer estivation and winter hibernation, and females must accumulate extra energy reserves for egg yolking. Grasses and other desert scrub plants are thought to be mostly secondary foods used only to support the tortoises' limited summer activity, but they may be more important than this, especially as a factor in the animals' annual energy budget (Peterson 1996b). Cacti (*Opuntia* sp.) may become important secondary foods and water sources in dry years (Turner et al. 1984).

In northern Arizona and southern Utah, Hansen et al. (1976) found that three grass genera (*Aristida* sp., *Tridens* sp., and *Bromus* sp.) amounted to 61% of the tortoises' diet. They also found sand, bird feathers, mammal hairs, snake and lizard skins, and arthropod parts in fecal scats. *G. agassizii* from southern Nevada fed on desert mallow (*Sphaeralcea* sp.) and plantain (*Plantago* sp.) 61% of the time. In the Sonoran Desert of Arizona, tortoises are known to eat 199 plant species, including herbs (55.3%, 39.7% of which are annuals), grasses (17.6%), woody plants (22.1%), and succulents (5%) (Van Devender et al. 2002). A small percentage of these plants are exotic invasive species that can make up an important part of tortoise diets at some places and seasons. More than half of the 43 major plant food species reported by Oftedal (2002) are found in both the Mojave and the Sonoran Deserts, yet only 8 of these are reported as major food items in both deserts. Oftedal concluded that the differences in diets between the tortoises of these areas are only partially attributable to regional differences in plant distribution.

At other sites, such as the western Mojave Desert of California, native plants are greatly preferred (Jennings 1997). Comparing food plants such as the exotic grass *Schismus barbatus* and the native forb *Sphaeralcea ambigua* reveals that the forb contains more nitrogen and water but less fiber than the grass. Because fiber is less digestible than other parts of plants (12.7 versus 10.7 kJ / g dry mass of the forb and grass, respectively), tortoises digest more dry matter and energy from the forb (Barboza 1995b). The nutritional quality of native and exotic invasive food plant species was investigated in more detail by Nagy et al. (1998). The native plants included a forb, *Malacothrix glabrata,* and a grass, *Achnatherum hymenoides.* The exotic plants included the forb *Erodium cicutarium* and the grass *Schismus barbatus.* Plants were collected during the time that they were available to tortoises (spring for forbs, summer for grasses) and then fed to penned tortoises. The measured proportions of plant components that were digestible were similar for both forbs and ranged from 63 to 70% for dry matter, 69 to 73% for energy content, 72 to 79% for nitrogen, and 70 to 75% for water. *Erodium* contains almost three times more nitrogen than *Schismus* and is 72% digestible. In contrast, *Schismus* does not contain enough digestible nitrogen to compensate for losses of nitrogen through defecation (Meienberger et al. 1993). Dry matter digestion amounted to 63% in *Erodium* and 50% in *Schismus,* and this corresponded to gross energy digestibilities of 69% and 48%, respectively.

Determining which forb is better from a nutritional standpoint requires assumptions (Nagy et al. 1998). If tortoises eat to simply fill their gut (Meienberger et al. 1993), the exotic species provides more digestible energy and nitrogen on a fresh mass basis; if they eat to meet their energy needs, the native plant provides more readily digestible nitrogen and water. The two grasses, with higher fiber content and significantly lower nitrogen content than forbs, have lower dry matter and energy digestibilities (46–50%). Tortoises on the grass diet (both native and exotic) lost more water than they gained and lost BM. Those that ate the native forb gained BM. Mean intake rates for the native forb were 3.5 g dry matter / day. Intake rates for the native grass were significantly lower, at 1.5 g dry matter/day. Not surprisingly, larger tortoises ate more food than smaller tortoises. Nagy et al. (1998) concluded that the type of food plant (forb or grass) and its phenological stage are more important determinants of the plant's nutritional value to tortoises than whether the species is native. This does not mean that invasive exotic plant species are inconsequential to tortoise diets. The ability of many exotic grasses to dominate landscapes and outcompete native plants in the Mojave Desert (Brooks 1999, 2000) means that tortoises will have potentially less high-quality native forage.

High-quality, more easily digestible, low-fiber diets are especially important to subadult tortoises. Tracy et al. (2006) fed juveniles either high-fiber or low-fiber diets and observed that the mean passage times for the solid portion of the diet were shorter for low-fiber diets, allowing for a potentially enhanced rate of nutrient extraction. For hatchlings, the passage time for low-fiber diets was just over 8 days and for the high-fiber diet was about 10 days. For one- to two-year-old juveniles, the low-fiber passage time was about 12 days, while high-fiber diets required about 13 days. Females with eggs consume less food than those that are not gravid (Meienberger et al. 1993).

Diet has a strong effect on the amount of food tortoises can eat (Meienberger et al. 1993). Comparing the two exotic plants *Schismus barbatus* and *Erodium cicutarium,* tortoises are able to eat about three times more *Erodium* between ingestion and passage of a digestive marker than those fed *Schismus* under experimental conditions. Tortoises that ate the forb gained BM during the study, while those that ate the grass lost a small amount of BM daily. The water content of *Erodium* averaged 75%, that of *Schismus* 7%. This difference does not affect fecal moisture under either diet (about 66%). Because grass is dryer than forbs under conditions when they are available to tortoises, large amounts of body water, about 1.0 g H_2O / g dry food intake, have to be invested during the digestion of grass. Water losses in fecal material on an *Erodium* diet are only 25% of the dietary intake of water. Tortoises that ate more had lower digestion transit times in the gut, which affected the digestibility of dry matter, gross energy, and cell wall components.

Martin and Van Devender (2002) recorded the diet and feeding behavior of *G. agassizii* in a peripheral Arizona habitat. Evidence of 50 plant species was found in the diet in the following general percentages: trees and shrubs, 4%; subshrubs, 10%; succulents, 6%; grasses, 30%; herbaceous perennials, 6%; and annuals, 44% (26% of which were spring obligates). The peak feeding period occurred from July to October, coincident with the monsoon rains, but tortoises were observed feeding from May to October. This sharply contrasts with the behavior of Mojave Desert tortoises, which feed primarily in the spring on annuals produced by winter rains. Fresh scat were found between May and 15 October; 57.1% of these scat were found in the summer and fall, but only 28.6% were found during late spring surveys. During the summer feeding peak, tortoises fed mostly on grasses (*Aristida* and *Bouteloua* sp.), taking lesser quantities of summer annuals including *Boerhavia intermedia, Euphorbia* sp., *Mollugo verticillata,* and *Portulaca oleracea,* fruits of *Opuntia engelmannii,* and some herbaceous perennials such as *Sida abutifolia.* Despite the presence of a diverse and widespread shrub and herbaceous perennial plant community, tortoises ate relatively little of those (except for *Calliandra eriophylla*). The limited feeding that occurred in the spring was mainly on annuals (*Astragalus nuttallianus, Lotus humistratus, Lupinus* sp., *Plantago patagonica*), and grasses (*Aristida* and *Bouteloua* sp.). The exotic plants *Bromus rubens* and *Erodium cicutarium* were also important foods, even when dry. The tortoises' diet generally tracked the seasonal availability of the various food plants; they switched to grasses and some warm season annuals in the summer.

Major tortoise food plants in the Mojave and Sonoran Deserts listed by Oftedal (2002) are as follows (not all plants in the list grow in both deserts, and those with an asterisk are introduced species): desert dandelions (*Malacothrix glabrata*), bright whites (*Prenanthella exigua*), small wire lettuce (*Stephanomeria exigua*), the nievitas (*Cryptantha angustifolia, C. circumscissa, C. micrantha, C. nevadensis*), combburs (*Pectocarya recurvata*), tansy mustard (*Descuraina pinnata*), peppergrass (*Lepidium lasiocarpum*), beavertail cacti (*Opuntia basilaris*), diamond chollas (*O. ramosissima*), rattlesnake weed (*Euphorbia albomarginata*), sandmat (*E. micromera*), twoseed milkvetch (*Astragalus didymocarpus*), Layne milkvetch (*A. layneae*), deer vetch (*Lotus humistratus*), longbract trefoil (*L. oroboides*), deer vetch (*L. strigosus*), filaree* (*Erodium cicutarium*), whitestem stickleaf (*Mentzelia albicaulis*), desert vine (*Janusia gracilis*), Indian mallow (*Abutilon* sp.), desert globemallow (*Sphaeralcea ambigua*), windmills (*Allionia incarnata*), wishbone bushes (*Mirabilis laevis*), woody bottlebrushes (*Camissonia boothii*), browneye primroses (*C. claviformis*), dune primroses (*Oenothera deltoides*), Indian wheat (*Plantago ovata, P. patagonica*), six-weeks threadawn (*Aristida adscensionis*), six-weeks grama (*Bouteloua barbata*), red brome* (*Bromus rubens*), cheatgrass* (*B. tectorum*), fluffgrass (*Erioneuron pulchellum*), bush muhly (*Muhlenbergia porteri*), Indian ricegrass (*Oryzopsis hymenoides*), big galleta (*Pleuraphis rigida*), Mediterranean grass* (*Schismus barbatus*), mesa dropseed (*Sporobolus flexuosus*), small fescue (*Vulpia microstachys*), and six-weeks fescue (*V. octoflora*).

During a wet year in the western Mojave Desert of California, the 10 preferred plants were hairy lotus (*Lotus humistratus*), four o'clock (*Mirabilis bigelovii*), rattlesnake weed (*Chamaesyce albomarginata*), Layne locoweed (*Astragalus layneae*), Egbertia (*Prenanthella exigua*), two-seeded milkvetch (*A. didymocarpus*), Booth's evening primroses (*Camissonia boothii*), stork's bill filaree (*Erodium cicutarium*), brittle spineflowers (*Chorizanthe bevicornu*), and lacy phacelia (*Phacelia tanacetifolia*). Forty-four species were eaten, but these 10 made up 81.4% of the diet. Not all plants flowered at the same time, leading to a large degree of variation in availability and selectivity. Tortoises selected certain plant parts and phenological stages, possibly for nutritional value, as demonstrated later (Jennings 2002). Avery and Neibergs (1997) studied the feeding ecology of desert tortoises in the eastern Mojave Desert of California. Major spring foods included *Camissonia boothii, Cryptantha angustifolia, Malacothrix glabrata, Opuntia basilaris, Rafinesquia neomexicana, Schismus barbatus,* and *Stephanomeria exigua.*

The energy content of food eaten by *G. agassizii* is about 16.6 ± 1.5 kJ / g dry matter for spring and fall diets and 16.8 ± 0.2 kJ / g dry matter in the summer. In September they ingested 20.2 g fresh food/kg daily and metabolized about 50% of the energy (Nagy and Medica 1986). Using the mean BM (2.7 kg) of *G. agassizii* from Iverson (1982a) and assuming that annual net primary production averages 14–43 g dry mass/m^2 in the Mojave Desert (Shreve 1925, *in* Congdon 1989), a single tortoise is theoretically capable of harvesting the annual plants on just over 1 m^2 in one day using the calculated September assimilation rate of Nagy and Medica (1986), assuming that production of food plants is homogeneous across the landscape (which it is not in the Mojave Desert; Rowlands 1986). The amount of dietary nitrogen necessary for survival was estimated to be 14.4 mg/kg$^{-0.75}$ a day, while a tortoise's digestible energy needs were estimated to be 19.9 kJ/kg$^{-0.75}$ a day (Barboza 1995b). These values underscore the modest nutritional needs of the tortoise in an unpredictable environment.

The mean retention times for large particles of grass and high-fiber pellets in the digestive system range from 14.2 to 14.8 days in the laboratory (Barboza 1995a). The quality and mineral content of potential food plants of the tortoise in southwestern Utah and northwestern Arizona were analyzed by McArthur et al. (1994), who found that plant mineral values did not generally mirror soil mineral values. Annual forbs were generally higher in mineral and nutrient content than perennial forbs, succulents, grasses, and shrubs. Sodium concentrations were low in both plants and soils.

Based on the numbers of bites taken during an El Niño year, juveniles in California's central Mojave Desert preferred *Camissonia claviformis, Oenothera primiveris,* and *Malacothrix glabrata. C. claviformis* accounted for 46% of all bites observed. The two most frequently encountered plants (*Cryptantha angustifolia* and *Schismus* sp.) were not the most frequently eaten. Even though *Schismus* sp. was encountered at about 7,100 individual plants/hour, it was significantly bypassed. Tortoises' feeding rate was estimated by counting the numbers of bites/hour. The mean rate was 159 (range, 49–301) bites of 17 plants/hour (Oftedal et al. 2002).

Juveniles demonstrate color choices when tested (Okamoto 2002). When presented with colored food pellets only, the order of preference was green, yellow, red, and orange. When presented with calcium supplements (eggshells and cuttlebone) in addition to colored food pellets, the order of choice was eggshells or cuttlebone, green, and yellow. When insects were presented along with colored food pellets, the choices were crickets, mealworms, and green. During the summer of 1991, Avery and Neibergs (1997) noted that tortoises in the eastern Mojave Desert of California selectively ate sphinx moth (*Hyles lineata*) larvae and that they were a greater source of water, crude protein, fat, and energy than were summer annual plants.

Limited food is available during the period of late summer hatching, and hatchlings spend little time on the surface (Luckenbach 1982). They dig their own small burrows or use an existing larger burrow. Dormancy follows shortly, probably before hatchlings have eaten or taken in water.

Luckenbach's (1982) observations of captive hatchlings suggest that they ignore food between the time of emergence and the beginning of winter dormancy; however, winter feeding has been observed in juveniles (Wilson et al. 1999a).

Marlow and Tollestrup (1982) observed females consuming the soil of a lime layer at an exposed site. The calcium content of this soil was significantly higher than that of adjacent areas, and all geophagous episodes involved reproductively mature females during the nesting season, a period when the females probably had their greatest calcium need for the shelling of eggs and for embryo shell and skeletal development. Nichols (1953) reported that captives will consume the eggs of their own species. However, calcium, like potassium concentrations in food plants, can be excessive compared to deficient elements such as phosphorus, sodium, and zinc, so additional hypotheses for geophagy should be examined (Oftedal 2002). Tortoises will also occasionally eat bones (including those of other desert tortoises; Walde et al. 2007a) and stones in addition to soil, possibly for the maintenance of gut pH, to control or eliminate the effects of secondary plant compounds that deter herbivory, to control intestinal parasites, or to maintain the shape and condition of the beak (Esque and Peters 1994). Juveniles may also eat caliche to gain access to minerals such as calcium carbonate (Stitt and Davis 2003). Henen (2002a) observed tortoises eating crytogamic soil containing the fungi *Collema coccophorum* and *Peltula* sp. at Goffs, California, although this constituted a very small portion of the food bites counted.

PREDATORS AND DEFENSE: Coyotes (*Canis latrans*), bobcats (*Lynx rufus*), mountain lions (*Felis concolor*), ravens (*Corvus corax*), golden eagles (*Aquila chrysaetos*), Gila monsters (*Heloderma suspectum*), and native fire ants (*Solenopsis* sp.) are known predators of various life stages of desert tortoises (Barrett and Humphrey 1986, Barrow 1979, Boone et al. 1999, Hensley 1950, Luckenbach 1982, Stitt et al. 2003), and ring-tailed cats (*Bassariscus astutus*), badgers (*Taxidea taxus*), skunks (*Conepatus mesoleucus, Mephitis macroura, M. mephitis, Spilogale gracilis*), kit foxes (*Vulpes macrotis*), gray foxes (*Urocyon cynereoargenteus*), domestic dogs (*Canis familiaris*), large hawks (*Buteo* sp.), owls (*Athene cunicularia*), roadrunners (*Geococcyx californianus*), and snakes (*Masticophis flagellum, Pituophis catenifer*) are implicated predators (Amarello et al. 2004; Averill-Murray et al. 2002b; H. Avery, personal communication; Ernst and Barbour 1972; Luckenbach 1982; Zylstra et al. 2005). The tick *Ornithodoros turcicata* is frequently an ectoparasite (Harbinson 1937, Ryckman and Kohls 1962).

The high density of ravens has a detrimental effect on populations through predation on young tortoises. Because the locations of raven nests change almost annually, there are few if any places in the desert where the potential for raven predation is low. Ravens prey primarily on tortoises <11 cm in SCL, pecking through soft parts of the shell and feeding on the viscera or pulling the head and limbs from the body. Large numbers of tortoise shells have been found under raven perches and nests, and this may reduce the number of small tortoises in populations associated with the presence of many ravens (Boarman 1993, 2003; Boarman and Coe 2002; Boarman et al. 2006; Kristan and Boarman 2003). In contrast, during two years of study near Twentynine Palms, California, ravens were not observed to be a source of mortality for hatchling tortoises (Bjurlin and Bissonette 2004).

Handling tortoises during research may cause mortality, especially during drought conditions (Berry et al. 2002b). Averill-Murray (2002b) observed decreased (5–13%) survival rates among tortoises that voided their bladders during handling by researchers in Arizona; however, recapture rates did not appear to be affected by urination. Decreased adult survival was not observed at a study site near Palm Springs, California (Lovich, unpublished data) where tortoises frequently voided when handled. The contents may be distasteful to a potential predator; Patterson (1971a) reported it puckered the mouth of a kit fox. If near a burrow, a tortoise will try to retreat underground when disturbed.

Barrett and Humphrey (1986) observed two agonistic interactions between adult female desert tortoises and Gila monsters that appeared to be digging for eggs at the entrances of tortoise dens. The females rushed, rammed, and nipped at the lizards and finally drove them away. These behaviors may have been cases of nest defense against egg predators. The fact that some Arizona females remain at their burrows 8–12 weeks following oviposition (Murray et al. 1996) may be related to defense of nests from marauding Gila monsters and other predators intent on eating their eggs; egg defense against both Gila monsters and humans has been reported by Averill-Murray et al. (2002a) and Zylstra et al. (2005).

Kit foxes were suspected as the predators that destroyed 12 (47%) of observed desert tortoise nests during two years of study in Twentynine Palms, California. Most nests were destroyed during the first 70 days of incubation. The canids' small size allowed them to ransack nests deep within the female tortoise's burrow. The mean clutch size of destroyed nests (5.9 eggs) was greater than that of surviving nests (4.3 eggs). All eggs in predated nests were consumed, with the exception of the eggs in a nest with one nonviable egg (Bjurlin and Bissonette 2004).

When molested, *G. agassizii* retreats into its shell, protecting its head with its forelimbs. It seldom bites but may release bladder water on a handler. Hatchlings differ from adults in their disposition; they can be pugnacious, advancing, hissing, and biting when touched; adults are generally rather docile (Booth 1958, Grant 1936, Marolda 2002). When threatened by raven models, neonates demonstrate plastral kinesis that decreases the size of their rear shell opening, even though they have no plastral hinge (Marolda 2002).

POPULATIONS: Although numerous estimates of desert tortoise population densities have been published, no one knows how many of these threatened animals are left in the wild or even how best to survey for them. Some authors surmise that at the time of listing the populations north and west of the Colorado River, there were far more than 100,000 tortoises alive (Freilich et al. 2000). This would surely make them one of the most abundant threatened or endangered vertebrates in the United States (Wilcove et al. 1993). Shortly after their listing under the ESA there was even disagreement on whether populations had declined enough to warrant protection (Bury and Corn 1995). The disagreement was based largely on the fact that earlier "evidence" of declines had not been peer reviewed or published in the scientific literature to allow scrutiny of the data. Uncritically reviewed estimates of historic densities of 1,000 and even more than 2,590 tortoises per square mile (summarized in Bury and Corn 1995) seem far-fetched in light of the rarity of tortoises described in accounts of early (1800s) expeditions in the desert Southwest.

Analysis of population data collected throughout Arizona and California from 1977 to 1989 (Corn 1994a) did not support the conclusion that tortoises were declining throughout the entire Mojave Desert but rather suggested that declines were most dramatic in the western Mojave, close to growing towns and cities. Declines in the western Mojave were corroborated by modeling population trend data (Doak et al. 1994). Disease may have been a factor in some of the study areas (discussed later). In the eastern Mojave Desert, populations appeared to be stable or increasing during the same time period. Regardless, the preponderance of published information suggests that most but not all tortoise populations north and west of the Colorado River have experienced some level of decline since that population was listed as threatened under the ESA in 1990. Elsewhere, tortoise populations in the Sonoran Desert of Arizona (Averill-Murray 2000) appear to be stable despite massive, recent increases in the human population and in recreational activity in tortoise habitat.

Tortoises can be difficult to sample because they spend so much time in burrows where they may be difficult to detect, especially in dry years (Freilich et al. 2000). In addition, tortoises often occur at low densities, often in a patchy distribution that is scale-dependent and more variable at small spatial scales (Krzysik 2002). Same-site surveys encompassing both wet and dry years can produce population estimates that vary by a factor of three (Freilich et al. 2000). Observer experience appears to have little effect on the ability to locate tortoises or tortoise sign (Anderson et al. 2001, Freilich and LaRue 1998), so skilled surveyors do not necessarily have greater detection rates.

Tortoise sampling falls into two basic categories, plot-based mark-recapture surveys and various types of transect-based surveys. Plot-based surveys typically use 1-mi^2 or 1-km^2 "study plots" (although smaller units of 0.25 km^2 or 1 ha have been used) that are surveyed for 60 days. During the time of sampling, all tortoises and tortoise sign (burrows, shells, scat) are counted and tortoises are marked. Various statistical methods (such as the Lincoln-Peterson Index) are then used to estimate the number of tortoises on the study plot. An advantage of this method is that detailed recapture data can be analyzed over time. A disadvantage is that extrapolation of density results to surrounding areas can be flawed due to the patchy distribution of habitats and tortoises in the desert.

Some earlier strip transect-based surveys used teams of people to walk and record sightings of tortoises and tortoise sign along triangular transects (see Grover and DeFalco 1995 for a summary of various techniques used). Densities were estimated based on 1-mi^2 "calibration plots" that were surveyed using the plot-based method described earlier. The assumption was that rates of sign detection were surrogates for and correlated with actual tortoise numbers, something that is not always true, especially for burrows (Rautenstrauch et al. 2002). Density estimates were difficult or impossible to generate with statistical confidence based on older strip transect data. A more modern adaptation of this technique is distance sampling, a rigorous, statistically robust method for determining density in an area by walking transects and measuring the distance from the line to any tortoises observed (Anderson et al. 2001, Buckland et al. 1993). Detection probability decreases with distance from the line because it is harder to see tortoises that are farther away (it is assumed that all tortoises on the line are detected). Once detection probabilities are generated for various distances, the method allows for a density estimate to be calculated. An advantage of this technique is that large areas can be surveyed; it is not limited to small plots (Anderson et al. 2001). However, it can be difficult to detect tortoises in the complex landscape of the Sonoran Desert. Despite this difficulty, distance sampling has been used successfully to sample tortoises in Arizona (Averill-Murray and Averill-Murray 2005).

Swann et al. (2002) used distance sampling to survey tortoises in the Rincon Mountains near Tucson, Arizona. The corrected mean density of tortoises in their rocky, hilly, 368.5-ha study area was 0.523 tortoises/ha. This corresponded to an estimated 193 tortoises at the entire site. When they used the Lincoln-Peterson mark-recapture estimator on their data, the tortoise population was calculated to be 224, which represented a substantial difference, especially considering that the confidence interval was double that based on distance sampling. Although the authors concluded that distance sampling can be used to effectively sample tortoises in Sonoran Desert upland habitats, they discovered that transects based on actual ground measurements resulted in 3% smaller abundance and density estimates than did transects based on mapped coordinates, a curious result.

Tortoise burrows and scat certainly indicate that tortoises may be in an area. Krzysik (2002) observed that although high counts of burrows and scat could be detected without finding a single tortoise, the opposite was never true. Duda et al. (2002) found strong correlations between both the numbers of total burrows and active burrows and actual tortoise abundance. They concluded that desert tortoise burrows can be used as effective surrogates for tortoise relative density patterns. Using burrows to estimate tortoise density can be especially valuable in dry years, when tortoises may not be surface active for periods long enough to allow their detection. Seasonal and sexual variation in the use of burrows complicates estimates of tortoise abundance from surrogate data (Rautenstrauch et al. 2002). Whatever method is used to estimate the abundance of desert tortoises, one thing is clear: it will be expensive. The U.S. Government Accountability Office (USGAO 2002) estimated that $7.5 million would be required in the first 5 years, plus an additional $1.5 million every 3 to 5 years over a total of at least 25 years, a time frame based on the recovery plan for the species written by the U.S. Fish and Wildlife Service (1994).

Population estimates can vary depending on what method is used. Schneider (1980) calculated the density of a California population using three capture-recapture methods. The Lincoln Index gave density estimates of 80–124 tortoises/km^2, the Schnabel Method estimates of 75–93/km^2, and the Stratified Lincoln Index estimates as high as 174 tortoises/km^2. A critical examination of the strengths and weaknesses of various survey techniques was presented by Freilich et al. (2005) using computer simulation based on actual tortoise location data from two 1-mi^2 study plots in southern California. Against this "known" distribution and abundance of tortoises on the plots, they subsampled the population at different plot sizes and by imposing simulated transects through the plots. Using 1-km^2 subplots did not produce estimates that were significantly different from those from the 1-mi^2 study plots, but 0.25-mi^2 subplots resulted in significant overestimates of populations. Simulations using distance sampling produced biased estimates 80% of the time and exhibited other undesirable statistical traits. Statistical power analysis indicated a limited ability to detect population declines of as much as 50%. The poor performance and bias of the two sampling procedures was due to insufficient sample size. The authors concluded that efforts must be directed at maximizing sample sizes in surveys in order to generate reliable estimates. Against this backdrop of uncertainty, we present earlier published estimates of tortoise densities based on surveys as variable as the number of publications! Even dogs have been used to survey for tortoises, successfully locating 90% of the experimental animals and finding smaller tortoises than human survey teams (Cablk and Heaton 2006).

Woodbury and Hardy (1948) found approximately 300 *G. agassizii* on about 486 hectares in Utah (0.62/ha; biomass, 2.05 kg/ha; Iverson, 1982a). Of the 281 tortoises they studied, 101 were males, 151 were females, 10 were of indeterminate sex but were thought to be equally divided between males and females, and the sexes of the remainder were unrecorded. They estimated that young tortoises made up less than 5% of the population and that the average annual rate of mortality was 1 to 5%.

Studies of 27 desert tortoise populations in southern California yielded additional density estimates. Berry (1986a) reported that 8 had estimated densities of 8 or fewer tortoises/km^2, 6 had 8–39/km^2, and 13 sites supported 42–184/km^2. Most sites had about equal numbers of nonadults (under 208 mm in CL) and adults (208 mm or more in CL). Samples from only 4 of 18 populations analyzed suggested that their sex ratios differed significantly from equality, similar to data from Arizona (Averill-Murray et al. 2002b). At Joshua Tree National Park, Freilich et al. (2000) captured 54 males, 61 females, and 50 juveniles and subadults for a density estimate of 42 adults/km^2. California populations studied by Barrow (1979) had densities of 0.29–0.31 tortoises/ha (biomasses, 0.59–0.64 kg/ha; Iverson, 1982a). At the Army's Fort Irwin National Training Center in the central Mojave Desert of California, Berry et al. (2006) estimated densities of <1 to 28 tortoises/km^2 on 21 study plots. The estimated densities were negatively correlated with the prevalence of clinical signs of mycoplasmosis, death rates estimated from shells and carcasses, surface disturbance from military training activities, and trash. Deaths from human activities, in turn, were strongly related to surface disturbances, trash, military ordnance, and proximity to settlements and roads. Other density estimates reported for southern California populations have been given by Berry et al. (1983), Bickett (1980), Luckenbach (1982), and Schneider (1980).

Densities in the Sonoran Desert of Arizona range from 5.8 to 57.9 tortoises/km^2, based on data from more than 20 localities. For the same populations, 95% confidence interval estimates range from 3.08 to 86.9 tortoises/km^2 (Averill-Murray et al. 2002b). Estimates from distance sampling in southwestern Utah ranged from 0.29 to 0.32 tortoises/ha (McLuckie et al. 2002). Most of the tortoises encountered were subadults or adults, and only 17% of the tortoises observed had CLs of less than 180 mm. Distance sampling in Arizona yielded estimates of only 0.23 tortoises/ha, but extrapolated over the entire Ironwood Forest National Monument, where the study was conducted, yields an estimate of 18,000 tortoises (Averill-Murray and Averill-Murray 2005).

Tortoises can contribute measurably to the biomass of their ecosystem. Data on desert tortoise densities north and west of the Colorado River range from 5 to 578/mi^2 (USFWS 1994). The standing crop biomass was estimated using the mean mass for individuals of the species (2.675 kg) calculated from the data of Iverson (1982) and ranged from 0.5 to 5.97 kg/ha.

Four populations (two from southern California and one each from Nevada and Utah) had similar values for the various size or age classes: 42–58% adults, 14–17% subadults, 18–33% juveniles, 5–10% very small tortoises, and only 1–2% hatchlings (Berry 1976). Size frequency distributions for three representative populations in Arizona tend to be bimodal and dominated by tortoises larger than about 22.0 cm in SCL and smaller than about 11.0 cm in SCL, with a distinct gap in the range of about 18.0 cm in midline SCL (Averill-Murray et al. 2002b).

The annual adult mortality rate is probably about 5% (Luckenbach 1982), but during very extended dry periods may rise to over 18% (Turner et al. 1984). The rate of survivorship of adults in the eastern Mojave Desert of California was about 88% per year (Turner et al. 1984). The rate of survivorship of adults in three populations in Arizona ranged from 94 to 97%, while that of juveniles less than 18.0 cm in SCL ranged from 84 to 93% (Averill-Murray et al. 2002b). At Joshua Tree National Park, Freilich et al. (2000) calculated an annual mortality rate of 0.117 and an annual recruitment rate of 0.092. Because these estimates were so close, they concluded that their population was stable from 1991 to 1995. Predator-induced mortality (see also Peterson 1994b) at the same study site in the drought year of 1997 resulted in significant mortality of adult females (Lovich, personal observation).

Germano (1994b) summarized data from various publications to estimate the rate of survivorship of tortoises from the western and eastern Mojave Desert. The percentage of eggs laid that hatched was 93% in the western Mojave and 46–67% in the eastern Mojave. The rate of survivorship from hatching to age one was estimated to be 51% in the eastern Mojave and from year one to maturity, 71–89%. The rate of adult survivorship in the western Mojave was 83.7–100%, while in the eastern Mojave it was estimated to be 75–98%. During a 34-day study investigating the movements and behavior of juveniles (6–8 yrs old) and neonates (<2 mo old) in the central Mojave Desert of California, there was no known mortality. All but one neonate survived from October to the following March (Hazard and Morafka 2002). In the southern Mojave, near Twentynine Palms, California, the rate of survivorship for hatchlings radio-tracked for 787 radio days was 88%. The rate of survivorship from egg deposition to the end of the study was about 40%, with mortality rates decreasing with neonate life stage (Bjurlin and Bissonette 2004).

Modeling population vital rates (e.g., survivorship, annual fecundity) in the western Mojave Desert of California suggests that population growth is more sensitive to the survival of large females than to that of any other segment of the population (Doak et al. 1994). Survival elasticities for *G. agassizii* were calculated by Heppell (1998). These elasticities measure the proportional contribution of vital rates such as age-specific survival and fecundity to the rate of population growth. The elasticities increased from juvenile to subadult to adult stages. This suggests that preadult survival elasticities contribute relatively less to the intrinsic population growth rate λ than do those of adults, providing additional support for the conclusion reached by Doak et al., that the survival of adults is important for population stability. This is at odds with the analysis of Congdon et al. (1993), who demonstrated that the population stability of long-lived animals such as tortoises is most sensitive to changes in adult or juvenile survival, while changes in age at sexual maturity, nest survival, or fecundity have lesser effects. Their results and those of Wisdom et al. (2000) suggest that it is important to protect all age groups of long-lived turtle populations.

Another important protected population of *G. agassizii* at the Desert Tortoise Research Natural Area, Kern County, California has declined since the 1970s, from 149 tortoises/km^2 to 75 tortoises/km^2 in 1989 (Berry 1991). Some of this mortality was due to upper respiratory tract disease (URTD) and raven predation on juveniles. In Piute Valley in southern Nevada, mortality from 1979 to 1983 significantly decreased both the mean SCL and the average age of the population but not the density, but by 1987 both average size and age had increased and density had remained stable (Germano and Joyner 1988). The annual mortality rate for hatchlings to 14-year-old juveniles was 14.5% between 1979 and 1983, while the rates for 15- to 25-year-old tortoises and for adults older than 25 years were 24.7% and 19.5%, respectively. From 1983 to 1987 the annual mortality rates for the three groups were 6.1%, 9.3%, and 10.3%, respectively. During both periods, the lower juvenile mortality rate ensured repopulation.

Drought conditions can contribute to mortality (Berry et al. 2002b) and are suspected of causing declines in populations in Arizona (Averill-Murray et al. 2002b) and California, especially among small (<18.0 cm in SCL) tortoises (Corn 1994a). During a drought lasting over two years in the eastern Mojave Desert of California, 41% of radio-tagged tortoises died from starvation and dehydration. During the same time frame, tortoises at a site in the western Mojave Desert experienced a 5–25% adult mortality rate, but the cause was suspected to be coyote predation and possibly disease, not drought conditions per se (Peterson 1994b). Longshore et al. (2003) simultaneously studied two populations in southern Nevada that were only 29 km apart. In spite of their proximity, the two sites had very different physiographies and rainfall patterns. One site varied from 290 to 360 m in elevation, while the other varied from 650 to 860 m. Drought began in the summer of 1995 and resulted in minimal or no production of annual plants in the springs of 1996, 1997, and 1999 at the lower site and 1996 and 1999 at the higher site. Survival rates at the two sites were similar in 1994 but diverged significantly thereafter. Seven-year survival rates, based on radiotelemetry, were 0.900 at the higher site and 0.269 at the lower site. The decline had all the appearances of a disease sweeping through the population, but no clinical signs of disease were observed. Extreme short-term drought conditions at the lower site appear to be responsible for the decline observed. Drought conditions at other sites may cause an increase in clinical signs of URTD in tortoises. Above-average rainfall conditions can result in a low percentage of tortoises presenting symptoms of this disease (Lederle et al. 1997). Thus, drought may kill tortoises indirectly by creating poor physiological conditions that result in greater impacts from exposure to pathogens.

Headstarting, or growing hatchlings under protected conditions until they are large enough to be released into the wild at a size less vulnerable to predation, has been advocated as a method for repopulating areas where tortoises are declining (Germano et al. 2002, Morafka et al. 1997). Translocation has also been used as a tool to replenish tortoise populations in areas that have experienced declines. At a site in Nevada, Corn (1994b) removed tortoises from their burrows in February and moved them 2 km away. The following year, all of the translocated tortoises were alive, and none exhibited signs of URTD. Field et al. (2007) used 32 tortoises that were relocated from developed areas of Las Vegas, Nevada, to test the effects of translocation. Animals were housed in seminatural conditions at the Desert Tortoise Conservation Center outside Las Vegas for periods of up to seven years before translocation. The translocation area was southwest of Las Vegas along Interstate 15. Many of the tortoises in that area were presumed to have been killed as they wandered onto the highway. Subsequent installation of tortoiseproof barrier fences (Ruby et al. 1994b) made the area suitable for translocation. As discussed under Behavior, translocated tortoises were from one of two treatments: water-supplemented and -nonsupplemented.

Following translocation, most of the tortoises (from both treatments) lost body mass until rainfall began in July. By the end of the study about one and a half years later, tortoises from both treatments were heavier, on average, than they had been prior to release. Body mass fluctuations between members of the two treatment groups were similar throughout the study. When data for both years of the study were combined, it was found that the mean CL of tortoises from the water-supplemented group increased significantly faster than that of tortoises from the nonsupplemented group. Movement patterns in 1997 (measured as straight-line distance and total distance moved) displayed some differences between sexes and treatments, with male water-supplemented tortoises moving significantly farther from the release site than males that did not receive supplemental water. These differences were not observed in 1998. The estimated mortality rate during the study was 21.4%, with all deaths occurring in 1997. Another 10.7% of the study animals were lost and thus assigned an unknown outcome (they could have either died or moved off of the study site), and another 67.9% were known to have survived. Because the translocation occurred in 1997 at the end of a period of low rainfall, the authors concluded that drought was more of a factor than translocation in their mortality results.

Although the results of the study by Field et al. are promising, Berry (1986a) cautioned that relocations may or may not be successful. According to her, wild populations possess dominance hierarchies, and to become established in areas where wild tortoises exist, released *G. agassizii* must displace residents, thus disrupting the local social structure. Failing in this, a newly released tortoise may be driven out by local residents. Relocated tortoises may settle at release sites, travel in straight lines (Type II navigation), or disperse for distances of more than 6 km; therefore, areas to be restocked should be at least 14 km in diameter (Berry 1986a). More recent studies found no evidence that the tortoises defended their territories (O'Connor et al. 1994b). However, longer-term data will be required to assess the success of translocation efforts.

Desert tortoise populations throughout much of their range, especially in the Mojave Desert, have experienced declines, and today the species is listed as threatened under the ESA in portions of all states in which it occurs. Mojave Desert populations north and west of the Colorado River were listed by the USFWS as endangered on 4 August 1989. Their status was changed to threatened on 2 April 1990. The USGAO (2002) estimated that more than $100 million has been spent on desert tortoise recovery actions since the species was first listed in 1980 (the Beaver Dam Slope population in Utah was listed as threatened at that time). Despite this large expenditure, few studies have been designed to evaluate the effectiveness of recovery actions (Boarman and Kristan 2006). The USFWS (1994) has provided additional information and actions that are recommended to recover the species from its threatened status.

Humans sometimes eat desert tortoises, run over them on our highways or with off-road vehicles, or shoot them (Berry 1986b, Bury and Marlow 1973, Luckenbach 1982). Large areas of tortoise habitat in the Mojave and Sonoran Deserts have been negatively affected by urbanization, off-highway vehicle use, overgrazing of domestic livestock, agriculture, construction of roads and utility corridors, and military training activities (Howland and Rorabaugh 2002, Krzysik 1997) and, more recently, by the deposition on the desert floor of litter in which the tortoise may become entangled or that it may swallow (Walde et al. 2007b). Secondary contributions to population degradation include the proliferation of exotic plant species and the higher frequency of anthropogenic fire and its negative effects on tortoises and their habitats (Brooks and Esque 2002; Esque et al. 2002, 2003). The effects of these impacts include alteration or destruction of macro- and microvegetation elements, establishment of plant communities dominated by exotic species, destruction of soil stabilizers, and soil compaction, erosion, and pollution (Lovich and Bainbridge 1999). Land use changes in the Mojave Desert ecosystem are projected to continue as human populations grow (Hunter et al. 2003), but examination of land use alternatives offers a tool to minimize impacts on the desert tortoise (Aycrigg et al. 2004).

Off-road vehicle (ORV) use is one of the human activities that is most widespread and destructive to desert habitat (Webb and Wilshire 1983), and tortoise populations have declined significantly in some areas of ORV use (Luckenbach 1982). ORV use may contribute to declines of tortoise populations directly by crushing individuals (above or below ground) or by collapsing burrows. ORV activity may also destroy vegetation used by tortoises for food or cover, making habitat unsuitable to sustain their populations. Two 25-ha plots in the western Mojave Desert of California, one a natural area and the other heavily used by ORVs, were sampled for tortoises by Bury and Luckenbach (2002). Comparing the two plots, the natural area had 1.7 times the number of live plants, 3.9 times the plant cover, 3.9 times the number of desert tortoises, and 4 times the number of active burrows relative to the ORV area. All differences were statistically significant. There were 1.25 tortoises/ha in the natural area and only 0.32 tortoises/ha at the ORV site.

ORVs are not the only form of transportation that affects desert tortoise populations. Several busy interstate highways cut through desert tortoise habitat and, together with the extensive network of other roads serving large western cities, create hazards for animals, including tortoises. The impact of road traffic on desert tortoise populations in southern Nevada was studied by von Seckendorff Hoff and Marlow (2002). The traffic levels on the roads studied ranged from 25 to 5,000 vehicles/day. Tortoises and tortoise sign decreased with proximity to the roads. Sign was reduced as far as 4,000 m from roads with the highest levels of traffic. There was a strong linear relationship between the traffic level and the total distance from the road that tortoise sign was reduced; roads with high traffic volume showed reductions of tortoise sign farther from the road edge, while roads with lower traffic volume showed reductions of tortoise sign nearer to the road edge. Tortoises will cross highways using culverts if they are passable (Boarman and Sazaki 2006, Boarman et al. 1998).

Artificial water sources, or "guzzlers," constructed in the desert for wildlife have been documented as a source of mortality for desert tortoises according to a 1993 memo in Lovich's files from the California Department of Fish and Game. Guzzlers provide water for bighorn sheep, deer, and other animals. The construction of some guzzlers (especially those made of fiberglass) is such that if a desert tortoise falls in it might not be able to escape and could ultimately drown. More recent surveys of 13 guzzlers in the Colorado Desert of southern California found the remains of several vertebrates, but no desert tortoises (Andrew et al. 2001). Additional surveys are necessary to determine the impact of these structures on desert tortoises.

Livestock may compete for food plants with desert tortoises, and livestock grazing may reduce tortoise populations (Berry 1978, Coombs 1979), although critical tests of these hypotheses are generally not available (Oldemeyer 1994). Avery and Neibergs (1997) demonstrated dietary overlap between cattle and tortoises in Ivanpah Valley, in the Mojave National Preserve in California, but overlap alone does not indicate competition. Certain key tortoise food plants may make up more than 40% of the cattle's diet, and because cattle are larger and more mobile than tortoises, these plants may be severely depleted with heavy grazing. In contrast, Bostick (1990) argued, based largely on circumstantial evidence and speculation, that the highest tortoise densities historically occurred at a time when livestock overgrazing was at its peak level and that the fewer the cattle on a range, the smaller the population of resident tortoises present. He suggested that the abundant cattle dung was a food source for tortoises. Later researchers demonstrated that cattle dung was a low-quality food source for desert tortoises (McArthur et al. 1994), and Avery and Neibergs (1997) showed that it was an insignificant part of the tortoise diet. Tortoises need food plants with high PEP indexes (see Behavior), which are abundant in high-rainfall years. Ironically, it may be more important to protect these plants from overgrazing by livestock in wet years, when it would appear that there is enough for both tortoises and livestock to eat, than in dry years. This is especially true in the Mojave Desert, where low levels of summer rainfall already stretch the potential limits of the tortoises' adaptation to desert environments. In the Sonoran Desert, the need for high–PEP index plants might be offset by food plants that germinate in response to summer rains (Oftedal 2002).

A comparison of the carapace bone composition in tortoises from grazed and ungrazed (cattle) habitats near the Arizona–Utah border revealed mild osteomalacia in tortoises from the grazed habitats (Wronski et al. 1992). This condition is caused by defective bone mineralization, but its effect on tortoises, if any, is unknown. Wronski et al. concluded that the location of their bone samples, the margin of the carapace, was not a good location for detecting bone abnormalities.

Disease appears to have contributed to declines of some desert tortoise populations (Berry 1997, Berry et al. 2006, Brown et al. 1999a, Christopher et al. 2003, Jacobson et al. 1994). Wild and captive desert tortoises are afflicted with URTD in many areas within their geographic range. A small bacterium (*Mycoplasma agassizii*) causes URTD in both desert and gopher tortoises (Brown et al. 1994, 2001; Jacobson et al. 1991), and another species, *M. testudineum*, has also been isolated from a desert tortoise with URTD (Brown et al. 2004). Introductions of infected captive tortoises into the desert may have caused the spread of this potentially lethal disease in wild tortoise populations. While URTD has been detected in desert tortoises in the Sonoran Desert of Arizona, the disease is not considered to have significant effects on populations there, and no deaths have been reported from it (Dickinson et al. 2002a). There is summer and winter rainfall in the Sonoran Desert but not in most of the Mojave Desert; this difference may be the factor that explains the health difference between tortoises in the two deserts. Some diseases may be linked to exposure to toxic elements such as mercury, lead, arsenic, and others (Seltzer and Berry 2005). Elevated levels of some of these, which are associated with mining activities, have been found in soils and some forage plants of tortoises (Chaffee and Berry 2006).

Exposure to the pathogens that cause URTD can be tested with enzyme-linked immunosorbent assay (ELISA) techniques (Schumacher et al. 1993). This technique detects antibodies in tortoises that have been exposed. It is important to note that exposure does not necessarily mean the tortoise displays clinical signs of infection, such as nasal and ocular discharge, and that clinical expression may be cyclical in individuals (Brown et al. 1999a). Schumacher et al. (1997) tested 144 tortoises with ELISA assays. Although 50% were seropositive for exposure to the pathogen, only 31% exhibited clinical signs of URTD. Seven tortoises had clinical signs but were seronegative. Overall, clinical signs of upper respiratory tract disease were positively correlated with ELISA results.

Johnson et al. (2006) found a positive correlation between clinical symptoms and the presence of antibodies produced after exposure to the disease, but Lederle et al. (1997) did not. In the latter study at the Nevada Test Site, 15–23% of the tortoises sampled tested seropositive but few showed clinical symptoms of infection. In a comparison of seropositive and seronegative female tortoises there were no significant effects of antibody status on reproductive parameters (Wallis et al. 1999). Tortoises at Goffs, California, with oral lesions are more likely to have positive nasal cultures for *Mycoplasma agassizii* than those without (Christopher et al. 2003). A majority of tortoises (8 out of 12) in the Las Vegas Valley that were considered to be healthy exhibited nasal lesions consistent with subclinical infections of URTD (Jacobson et al. 1995). Females can pass antibodies for exposure to URTD to their offspring via egg yolk (Schumacher et al. 1999), but these may not be able to protect them from subsequent exposure to the disease. There is no evidence of transmission of URTD from females to their embryos.

Disease may be spread by release of infected captive tortoises back into natural habitats (Jacobson 1993, Johnson et al. 2006). Evidence in support of this finding was presented by Berry et al. (2006), who found a negative relationship between the occurrence of clinical signs of the disease and distance from human settlements and paved roads at the Army's Fort Irwin National Training Center in the central Mojave Desert of California. In other words, areas remote from human activities were less likely to contain infected tortoises.

Another disease, cutaneous dyskeratosis, has been implicated in the decline of tortoises on the Chuckwalla Bench in the Colorado Desert of California (Jacobson et al. 1994). The disease is characterized by lesions on the scutes of the carapace, plastron, and forelimbs that spread from the seams toward the center of the scutes. Diseased parts appear as gray-white and sometimes orange areas, with a rough, flaky appearance (Homer et al. 1998). The protein composition of scutes may be altered between healthy and sick tortoises (Homer et al. 2001). Some of the tortoises in the area are missing scutes and show exposed bone, while others appear to be healthy and normal (Lovich, personal observation). The exact cause of the disease is unknown. Other potential pathogens of desert tortoises include *Pasteurella testudinis*, *Pseudomonas* spp., *Salmonella* spp. (Dickinson et al. 2001), and even herpesviruses that cause other ailments (Jacobson 1994, 2002; Johnson et al. 2005; Pettan-Brewer et al. 1996). Guidelines for field evaluation of desert tortoise health are provided by Berry and Christopher (2001).

Berry (1997) reported declines, assumed to be caused by URTD and cutaneous dyskeratosis, in two widely separated tortoise populations in California. At the Desert Tortoise Research Natural Area in the western Mojave Desert, a marked study population declined from 75 tortoises/km^2 in 1979 to 18 tortoises/km^2 in 1992. At the Chuckwalla Bench in the Colorado Desert, another marked population declined from 153 tortoises/km^2 in 1982 to 70 tortoises/km^2 in 1992.

REMARKS: Morafka and Berry (2002) presented a hypothesis for the evolution of *G. agassizii* suggesting that the ancestors of desert tortoises evolved from Asian geoemydines and that tortoises are simply a specious lineage of that group, not a family in their own right. Either manourine tortoises in particular gave rise to North American tortoises or they are a sister clade (which is supported by data on their phalangeal formulae; Crumly and Sánchez-Villagra 2004).

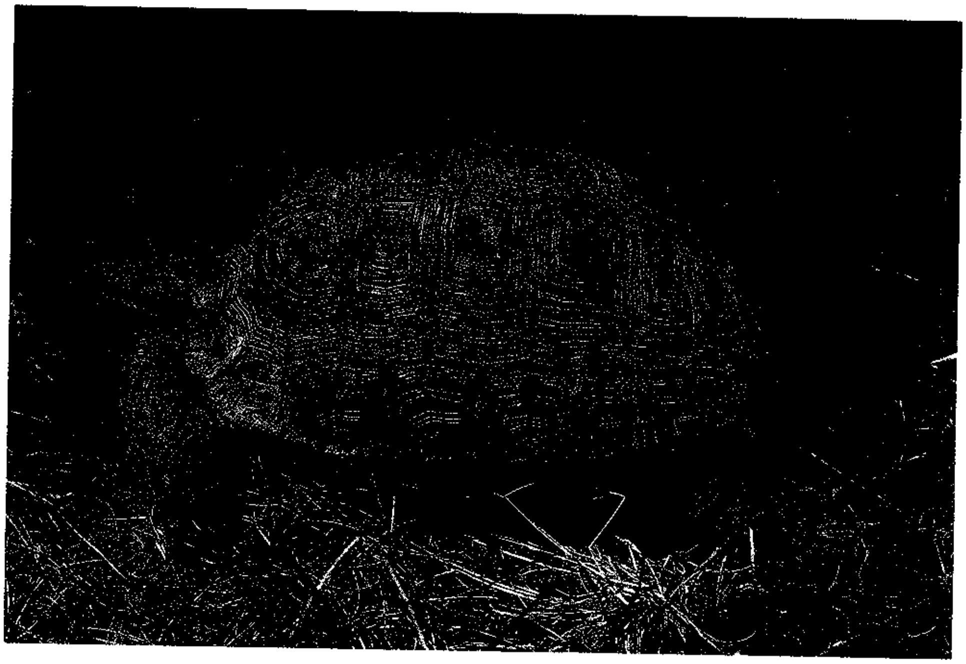
Some traits and behaviors of the desert tortoise that are considered adaptations to the aridity of the desert are likely to be exaptations—adaptations that evolve in one context but predispose the organism to another set of challenges—that evolved in their forest-dwelling ancestors in Asia. For example, burrowing, a well-developed trait in the desert tortoise, may have initially evolved to protect animals from high levels of heat in edge habitats but later served to protect their descendants from extreme cold and predators. In addition, morphological adaptations for burrowing may have evolved in a grassland or forest ecotone and later served the tortoise after the climatic evolution of modern deserts. The ancestors of *G. agassizii* may have appeared 17–19 million years ago, perhaps 12 million years before the formation of the North American deserts. Modern *G. agassizii* likely appeared within the past 3–5 million years, but modern desert climates and vegetation formed during the past 1% of that time period, mostly in the past 7,000 years! This and other information summarized by Morafka and Berry (2002) suggested that the "desert" tortoise became associated with desert conditions only in recent geological time. Further information on the evolution of the genus *Gopherus* is summarized in the accounts of Testudinidae, the *Gopherus* genus, and *G. berlandieri* in this book. Additional details on the evolution of *G. agassizii,* in particular, are found in the works of McCord (2002) and Van Devender (2002c).

The morphology and staining characteristics of desert tortoise blood cells and hematopoietic cells are discussed by Alleman et al. (1992) and Garner et al. (1996), respectively, and the physiological parameters of healthy tortoises are reported by Christopher et al. (1999) and Dickinson et al. (2002b). Their internal morphology, as revealed through ultrasonography, is discussed by Penninck et al. (1991).

An excellent treatment on the natural history of tortoises in the Sonoran Desert is provided by Van Devender (2002a), and compendia on North American tortoises, including *Gopherus agassizii,* are found in the works of Bury (1982) and Bury and Germano (1994). For further information and lists of references on *G. agassizii,* see the works of Auffenberg and Franz (1978b), Douglass (1975, 1977), and Grover and DeFalco (1995) and the *Proceedings of the Desert Tortoise Council.* Some authors have criticized papers in the latter as "gray literature," since they were not peer reviewed (Germano and Bury 1994), and have advocated a more rigorous approach to acquiring knowledge for this species. Nevertheless, there are some classic papers in that series that provide excellent summaries regarding aspects of desert tortoise biology. Although the literature on the desert tortoise was primarily gray prior to the animal's listing under the Endangered Species Act (Germano and Bury 1994), the peer-reviewed literature on the desert tortoise exploded after that, making it one of the best studied turtles in the United States.

Gopherus berlandieri (Agassiz, 1857)
Berlandier's Tortoise

Berlandier's tortoise is the smallest of the North American members of the genus *Gopherus.* It has become much better known since the last edition of our book, particularly



Gopherus berlandieri
(C. H. Ernst)

EXHIBIT 457

Conservation Biology

Review

Suitability of Amphibians and Reptiles for Translocation

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Abstract: *Translocations are important tools in the field of conservation. Despite increased use over the last few decades, the appropriateness of translocations for amphibians and reptiles has been debated widely over the past 20 years. To provide a comprehensive evaluation of the suitability of amphibians and reptiles for translocation, we reviewed the results of amphibian and reptile translocation projects published between 1991 and 2006. The success rate of amphibian and reptile translocations reported over this period was twice that reported in an earlier review in 1991. Success and failure rates were independent of the taxonomic class (Amphibia or Reptilia) released. Reptile translocations driven by human–wildlife conflict mitigation had a higher failure rate than those motivated by conservation, and more recent projects of reptile translocations had unknown outcomes. The outcomes of amphibian translocations were significantly related to the number of animals released, with projects releasing over 1000 individuals being most successful. The most common reported causes of translocation failure were homing and migration of introduced individuals out of release sites and poor habitat. The increased success of amphibian and reptile translocations reviewed in this study compared with the 1991 review is encouraging for future conservation projects. Nevertheless, more preparation, monitoring, reporting of results, and experimental testing of techniques and reintroduction questions need to occur to improve translocations of amphibians and reptiles as a whole.*

Keywords: herpetofauna, population supplementation, reintroduction, relocation, repatriation, translocation

Aptitud de Anfibios y Reptiles para la Translocación

Resumen: *Las translocaciones son herramientas importantes en el campo de la conservación. No obstante el incremento de su uso en las últimas décadas, la efectividad de las translocaciones de anfibios y reptiles se ha debatido ampliamente en los últimos 20 años. Para proporcionar una evaluación integral de la aptitud de anfibios y reptiles para la translocación, revisamos los resultados de proyectos de translocación de anfibios y reptiles publicados entre 1991 y 2006. La tasa de éxito de las translocaciones de anfibios y reptiles reportada en ese período fue el doble de la reportada en una revisión previa en 1991. Las tasas de éxito y fracaso fueron independientes de la clase taxonómica (Amphibia o Reptilia) liberada. Las translocaciones de reptiles dirigidas por la mitigación de conflictos humanos-vida silvestre tuvieron una mayor tasa de fracaso que las motivadas por la conservación, y los proyectos más recientes de translocación de reptiles no tienen resultados conocidos. Los resultados de translocaciones de anfibios estuvieron relacionados significativamente con el número de animales liberados, los proyectos que liberaron más de 1,000 individuos fueron más exitosos. Las causas más comunes de fracasos de translocación fueron el regreso al hogar y la migración de individuos introducidos fuera de los sitios de liberación y hábitat inadecuado. En comparación con 1991, el incremento del éxito de las translocaciones de anfibios y reptiles revisadas en este estudio es alentador para futuros proyectos de conservación. Sin embargo, se requiere mayor preparación, monitoreo, reporte de resultados y experimentación de técnicas y preguntas de reintroducción para mejorar las translocaciones de anfibios y reptiles en conjunto.*

Palabras Clave: herpetofauna, reacomodo, reintroducción, repatriación, suplemento de la población, translocación

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Introduction

Translocations are an important tool in wildlife conservation (Griffith et al. 1989; Dodd & Seigel 1991; Fischer & Lindenmayer 2000). Thousands of translocations have occurred worldwide, although most of these have been taxonomically biased toward vertebrates, especially mammals and birds (Seddon et al. 2005). One group that has been overlooked in larger reviews of translocation programs, but which stands to reap substantial benefits from such techniques, is herpetofauna.

With further documentation of the worldwide amphibian decline and the extinction of a number of amphibian and reptile species, it is clear that proactive conservation is needed (Gibbons et al. 2000; Stuart et al. 2004; Mendelson et al. 2006). As a part of this, both translocations of wild individuals and projects coupled with captive-breeding programs appear to be growing in popularity. Furthermore, the recent Amphibian Conservation Summit listed translocations as one of 3 long-term conservation programs requiring development and implementation in the Amphibian Conservation Action Plan (Gascon et al. 2007). In addition to conservation-related motives, many other herpetofaunal translocations are being conducted to deal with human–wildlife conflicts, such as “problem” animals or building and development mitigation.

In a review of amphibian and reptile translocations, Dodd and Seigel (1991) found that amphibian and reptile projects have very low success rates, especially compared with translocations of other taxa, and they suggest that amphibian and reptile species are not suitable for translocation. Since the publication of their review, there has been wide debate in the literature (Burke 1991; Dodd & Seigel 1991; Reinert 1991; Seigel & Dodd 2002; Trenham & Marsh 2002). Despite their questionable suitability for translocation and that many amphibian and reptile species continue to undergo translocation, there has been no comprehensive review of amphibian and reptile translocations since 1991.

To improve management decisions, successes and failures of past programs need to be considered. We reviewed the results of programs published in scientific journals from 1991 to 2006 to reevaluate the suitability of amphibians and reptiles for translocation. In addition, we examined trends that may indicate key factors leading to the success or failure of projects.

Definition of Terms

Several terms have been used to refer to the release of animals into former areas within their range, including *reintroductions*, *translocations*, *relocations*, and *repatriations* (Griffith et al. 1989; Reinert 1991; Dodd & Seigel 1991; IUCN 1987, 1998). Because these terms have been used inconsistently in the literature, a recent call has been made to return to the original International Union for Conservation of Nature (IUCN) definitions outlined in the 1987 IUCN translocation position statement (Armstrong & Seddon 2008). We followed these IUCN definitions and use the term *translocation* to mean any movement of living organisms from one area to another. This includes deliberate movements of animals to establish a new population, reestablish an extirpated population, augment a critically small population, or mitigate for conflicts between animals and humans (Griffith et al. 1989; Wolf et al. 1996; Wolf et al. 1998). For the purpose of this review, we did not include releases and introductions of animals outside their natural range.

Although many projects report success, often what is being reported is only a short-term success. The ability of released animals to successfully overwinter, create burrows, or remain within a protected area does not, by itself, constitute a successful translocation program. A successful program produces a viable, self-sustaining population in the wild (Griffith et al. 1989; Dodd & Seigel 1991; IUCN 1998), and the population must be monitored for a sufficient amount of time to determine that it is self-sustaining. The amount of time necessary to do this may vary from several years for short-lived species to several decades for long-lived species (Dodd & Seigel 1991).

Here, we considered a translocation project a success if it met 2 criteria: there was evidence of a substantial addition of new recruits to the adult population due to successful reproduction at the translocation site, and the site had to have been monitored, at the very least, for the amount of time it takes that species to reach maturity. The outcome of a program was considered uncertain if monitoring time was inadequate or if there were too few data to classify it as a success or failure. We ranked projects as failures if they did not establish self-sustaining populations.

Methods

We reviewed amphibian and reptile translocation projects published in the scientific literature from 1991 to 2006, although some of the actual projects were carried out as early as the 1970s. Reports published before 1991 have been reviewed elsewhere (Dodd & Seigel 1991). We used electronic databases, reference lists, and personal contacts to find articles. Sea turtles were deliberately excluded because of the large number of projects concerning head-starting and release programs and the difficulty in relating the issues involved with their release to terrestrial and freshwater herpetofauna.

We attempted to determine the following factors for each project: species or taxonomic group being relocated; geographic region (North America, South America, Africa, Europe, Asia/Oceania) of the translocation; reason for translocation; date of release; whether founder individuals were from the wild or captivity; number of animals released; life stage of released animals (eggs, larvae, metamorphs, juveniles, subadults, adults); success of the project (as determined on the basis of our criteria); and cause of project failure.

Because of the nature of the data collected, we present the results with descriptive statistics in histograms to help illustrate trends. If a project fits into more than one category for a variable (i.e., if a project released both juvenile and adult animals), then it was counted twice. Therefore, total *n* may be greater than the total number of projects reviewed. Percentages are of the total *n*, which included projects of known (successes and failures) and uncertain outcomes.

We tested for the independence of outcomes in relation to variables with chi-square tests. For chi-square tests, we compared only projects with known outcomes (success or failure). The exception to this rule was in our evaluation of the time period (decade) during which translocations took place, for which we compared projects that succeeded, failed, and had unknown outcomes. When a contingency table had at least one expected cell frequency <5 and a chi-square test could not be used, we used a Fisher's exact test to compute a probability. Significance levels were set at $\alpha = 0.05$.

Results

We reviewed 91 translocation projects that covered 25 amphibian species and 39 reptile species. A complete table of all projects reviewed together with appropriate references is available from www.otago.ac.nz/zoology/staff/academic/bishop.html. Six of the 91 projects involved restocking into existing populations (also known as augmentation) and were not included in the main analyses, but are discussed separately. Of the 85 amphibian and reptile translocations, 38 projects (45%) consisted of translocations of amphibians and 47 projects (55%) involved reptiles. Thirty-six of these combined projects (42%) were successful. For 25 projects (29%), the long-term success was still uncertain, whereas 24 projects (28%) failed. Success and failure rates were independent of the taxonomic class (Amphibia or Reptilia) released ($\chi^2 = 0.545$, df $= 1, p = 0.460$; Fig. 1).

To determine whether there were any differences over time in the known and unknown outcomes of programs (success, failure, and uncertain) published since 1991, we sorted the projects into decades on the basis of when the translocation occurred. For amphibians, program outcome was independent of the decade during which the translocation was carried out ($p = 0.204$). Project results for reptiles, however, were tied to the decade in which they were carried out ($p = 0.009$), with projects carried out in recent years having higher proportions of uncertain outcomes (Fig. 2).

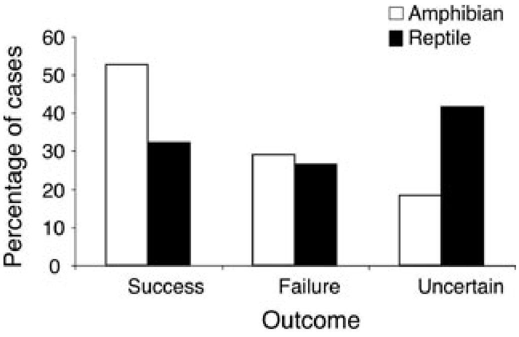

Figure 1. Outcomes of translocation projects for 38 amphibian and 47 reptile projects.

The specific reasons for translocating a species varied greatly, but could generally be grouped into one of the following: conservation, research, or human–wildlife conflict (which included development mitigation and dealing with problem animals). For amphibians, the majority of translocations were carried out for conservation reasons (89.5%), and human–wildlife conflict motivations (7.9%) and research (2.6%) made up only a small proportion of the overall reasons for carrying out a release. In the case of amphibians, the success or failure of translocations was unrelated to the reasons for conducting the release ($p = 0.480$). For reptiles, although conservation was still the leading motivation for translocation projects (74%), research projects and projects motivated by human–wildlife conflict made up 10 and 16% of the projects reviewed, respectively. Furthermore, for reptile translocations with known results, the project outcome was correlated with the program motivation ($p = 0.006$). Reptile projects carried out to deal with

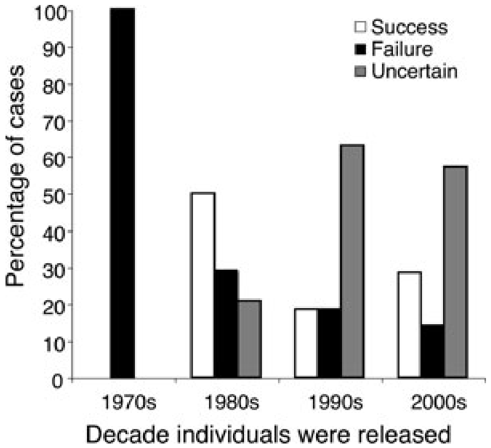

Figure 2. Outcomes of reptile translocations on the basis of the decade of animal release (1 project from 1970s, 23 from 1980s, 22 from 1990s, and 7 from 2000s).

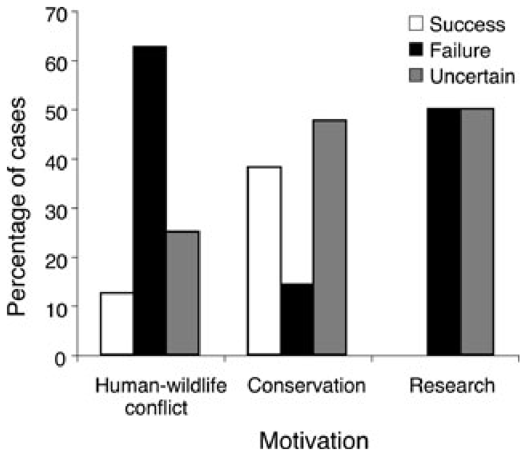

Figure 3. Outcomes of reptile translocations on the basis of motivation for the translocation (38 projects motivated by conservation reasons, 5 by research, and 8 by human–wildlife conflicts).

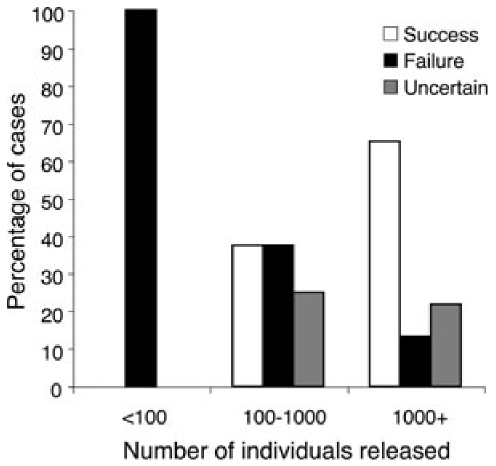

Figure 4. Outcomes of amphibian translocations on the basis of the number of individuals released (3 projects for <100 individuals, 8 projects for 100–1000 individuals, 23 projects for over 1000 individuals).

human–wildlife conflicts had the highest failure rates of the 3 motivations, whereas conservation-driven projects had the highest success rates (Fig. 3).

Most herpetofaunal translocation projects were carried out with wild individuals, with 76% of amphibian translocations and 93% of reptile translocations carried out with only wild animals. Most reptile translocations in which captive animals were used had, at present, uncertain outcomes; thus, it was not possible to determine whether the source of animals translocated had an impact on the success of the project. Nevertheless, in the case of amphibians, the source of animals reintroduced (wild, captive, or a combination) was independent of the project outcome ($p = 0.310$).

Translocation outcome was independent of life-stage category of released animals for both amphibians ($p = 0.683$) and reptiles ($p = 0.312$). Nevertheless, amphibian and reptile translocation projects used different age groups for release. For amphibians, 71% of the projects included the release of eggs, larvae, and metamorphs and 45% included the release of adults. Only 21% of amphibian translocations released juveniles. For reptile translocations, 64% of the projects incorporated the release of juveniles and subadults and 75% released adults. Only 4% of reptile translocations included the relocation of eggs.

Location had no effect on the outcome of translocations in both amphibians ($p = 0.141$) and reptiles ($p = 0.10$). The greatest number of publications on translocations were from North America for both amphibians (23 projects) and reptiles (32 projects). Australasia had the second-greatest number of publications on reptile translocations (9 projects) and Europe was second in the number of publications on amphibian translocations (9 projects).

For amphibian translocations, the number of animals released significantly affected success rates ($p = 0.008$); projects releasing over 1000 individuals were more successful than those releasing less than 100 or 101–1000 individuals (Fig. 4). The number of individuals released in reptile translocations (0–50, 51–100, or >100 individuals) was independent of project outcome ($p = 0.639$).

Of the reported causes of failure, the most common for amphibians and reptiles were homing, large movements, and migration away from the release site. Other factors, such as insufficient numbers and poaching or human collection, were evident in both failed amphibian and reptile translocations (Fig. 5). In many projects, however, the cause of failure was unknown or not reported.

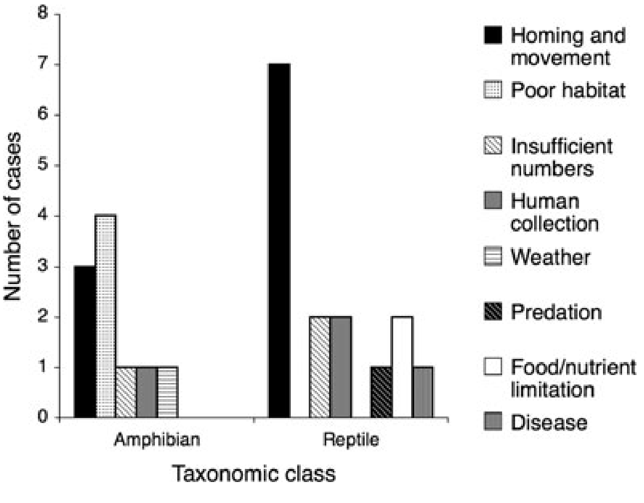

Figure 5. Reported causes of failure of amphibian and reptile translocation projects.

Of the 6 cases of restocking, 4 were carried out for conservation and 2 for research purposes. Of the conservation-motivated projects, 2 were successful and 2 had uncertain outcomes.

Discussion

Overall Review of Amphibian and Reptile Translocation Results

The proportion of successful amphibian and reptile translocation projects (41%) we reviewed from the past 15 years is double that previously reported for herpetofaunal translocations (19%; Dodd & Seigel 1991). This increase in positive results is an encouraging sign for the management and conservation of amphibians and reptiles. Nevertheless, this figure is within a similar range of reported success rates from reviews of translocations across all animal taxa (Griffith et al. 1989; Wolf et al. 1998; Fischer & Lindenmayer 2000). Even with the increase in success rates of amphibian and reptile translocations, the current figures demonstrate that room for improvement remains.

Publication bias and the reluctance of authors to report failed translocations may have caused an overestimation of true success rates (Dickerson & Min 1993; Scargle 2000). Without access to information on failed translocations, conservation managers and researchers cannot make informed decisions about the techniques to be used in future translocations.

Another issue to consider is that translocations can take years, if not decades, of monitoring to determine whether or not the project was successful. When looking at the long-term success ratings of projects by decades, the trend is that the proportion of projects with uncertain outcomes has risen dramatically in more recent projects, especially for reptiles, which include a number of long-lived and slow-to-mature species. It is nearly impossible to compare the differences in success rates of recent projects when the outcomes of such a great number of projects are unknown. Nevertheless, it does emphasize the importance of long-term monitoring. For many translocation programs, it can take 15–20 years before success can be reliably evaluated (Dodd & Seigel 1991; Nelson et al. 2002; Bell et al. 2004).

Long-term monitoring is necessary for the evaluation of projects and to determine if intervention is needed for the survival of relocated populations (Seddon 1999). Many researchers have advocated for better monitoring (Griffith et al. 1989; Dodd & Seigel 1991; Seddon 1999; Fischer & Lidenmayer 2000), and it is vital that all organizations carrying out translocations commit to the long-term monitoring essential for these projects.

Motivations for Translocation Projects

By far the greatest numbers of translocations for both amphibians and reptiles have been performed for conservation reasons. Although research and the mitigation of human–wildlife conflicts are motivations for a few amphibian projects, in reptiles they make up 16% of projects carried out. In addition, the reason behind reptile translocations was significantly linked to the project's outcome, and reptile projects carried out for conservation had the highest success rates and those driven by human–wildlife conflict were the least likely to meet our criteria for success. This trend was not found in amphibian translocations, perhaps because the sample size of nonconservation-driven projects was small.

Translocations driven by human–wildlife conflicts were usually carried out either as a mitigation effort for development projects or to transfer species that are deemed potentially dangerous to humans. Although these were some of the most unsuccessful projects reviewed, our estimates are probably conservative because it is likely that the results of many of these projects are not being reported. Companies involved in translocations for mitigation purposes may not monitor projects after release and may not report failure rates due to the fear of negative publicity (Edgar et al. 2005; Teixeira et al. 2007). In addition, outside the transfer of a population, factors such as a net loss of habitat or the quality of new habitat created for translocated animals may not currently be taken into consideration by mitigation projects. For instance, a review of great crested newt translocations used for development mitigation in the United Kingdom showed that although new ponds were created to compensate for lost ponds, the overall habitat area available to the newts had decreased (Edgar et al. 2005).

In translocations motivated by human–wildlife conflict, the survival of released animals was poor (Walsh & Whitehead 1993; Hare & McNally 1997; Rathbun & Schneider 2001; Sullivan et al. 2004; Butler et al. 2005*a*, 2005*b*). The majority of translocations of problem carnivore species, most of which were mammals, met with the same poor results for many of the same reasons as in the projects for amphibians and reptiles driven by similar motives (Linnell et al. 1997). Translocations are not an easy solution to these problems and should not be suggested as a first step in dealing with the conflicts between people and animals.

Problem animals and animals whose habitats are to be developed for human use need to be dealt with either through preventative measures or by holding the organizations moving the animals accountable for the results. If animals must be moved for development mitigation, it is essential to consider the strong homing instincts of herpetofauna and the need for appropriate release habitat both in size and quality.

Factors That Influence Translocation Success

Reviews of translocations of other taxa show that several factors often led to more successful programs. One of these has been the source of founding individuals, with translocations of wild animals being more successful than translocations of captive animals (Griffith et al. 1989; Fischer & Lindenmayer 2000). This does not appear to be the case with amphibians because the success rate was similar for wild and captive releases.

A number of traits make amphibians and reptiles good candidates for captive-release programs, including high fecundity, lack of parental care, and that numerous small-sized amphibian and reptile species can be bred in captivity in a very cost-effective manner (Bloxam & Tonge 1995). In addition, captive-bred mammals may lose natural behaviors in captivity, but some amphibians and reptiles seem to retain in captivity behavioral and physiological traits that are genetically programmed. For instance, several tests on captive rattlesnakes showed their strike-induced chemosensory searching behaviors were similar to those of wild snakes (Chiszar et al. 1993). In addition, approach distances of headstarted West Indian iguanas after release into the wild did not differ from those of wild animals of the same age, which shows they retained similar antipredator behaviors (Alberts et al. 2004). Although the source of release individuals may be less of an issue for herpetofauna than for mammals and birds, more releases are still composed of wild individuals than captive ones.

Although we found no significant difference in the outcomes of wild and captive translocations, the release of individuals held or bred in captivity added a number of issues that must be considered. It is crucial that disease risks associated with captive-breeding and release programs be considered. The risks that the released animals will transmit diseases and new parasites to wild populations and that inbreeding depression and acclimation may result in the inability of released animals to deal with such challenges in the wild (Jacobson 1993; Cunningham 1996). Recent tests of the fitness of captive-bred and wild toads show that important fitness attributes and high levels of heterozygosity can be maintained for several generations in captivity (Kraaijeveld-Smit et al. 2006). Nevertheless, other work shows that captivity can change the phenotype of animals, which may have implications for their ability to cope in a natural environment (Connolly & Cree 2008). If captive animals are to be released into the wild, these issues must be taken into account.

Another important factor to consider for translocation programs is the developmental stage of released animals. Although we found no difference in success rates, the results of several studies do suggest that certain age groups are more appropriate for translocation than others (Bloxam & Tonge 1995; Cooke & Oldham 1995; Trenham & Marsh 2002; Tocher & Brown 2004; Tocher et al. 2006). When dealing with species that show strong homing tendencies, it may be beneficial to release eggs or younger individuals rather than older adults that have had sufficient time to develop strong associations with a home site (Gill 1979; Bloxam & Tonge 1995; Semlitsch 2002; Tocher & Brown 2004). In addition, for aquatic-breeding amphibians, it may be preferable to move eggs or animals in early larval stages due to the large numbers available, which aids in ease of collection and maximizes genetic diversity. In addition, in aquatic amphibians, eggs are often available for collection from the wild for longer periods than adults, which may appear only at breeding locations for short periods (Semlitsch 2002). For many species, however, the greatest threats to individual survival come at younger life stages, when animals are more vulnerable to predators and the normal dangers of life in the wild and in these projects, so it may be better to release adults or large juveniles (Haskell et al. 1996; Nelson et al. 2002; Alberts 2007). This is particularly useful in the case of herpetofaunal species restricted to islands, where the main cause of juvenile mortality is caused by introduced mammals (Nelson et al. 2002; Alberts 2007). Outside the species-specific and logistical choices of whether to release eggs, juveniles, or adults, there is little—if any—experimental work that tests the suitability of different herpetofaunal age classes for translocation programs and the effect of developmental stage on outcomes.

A number of amphibian and reptile translocations have failed because of the release of insufficient numbers of animals (Cook 2008). When release numbers are too small, Allee effects may come into play, and the new population may fail owing to problems associated with social behavior, finding mates, and group living (Courchamp et al. 1999; Stephens & Sutherland 1999). For amphibians, translocation projects that released over 1000 individuals were the most successful, although we found no correlation between release number and outcome of reptile translocations.

For aquatic amphibians Semlitsch (2002) suggests the release of 10,000–50,000 eggs over several years to reach an adult population of 100 individuals. Nevertheless, for most herpetofaunal species, there is no easy number to use as a guideline. Several amphibian translocation programs used population modeling as a tool to make recommendations on the optimal number of animals to be captured and released (Geraud & Keinath 2004; Tocher et al. 2006). These models are most useful for species for which adequate population and life-history data are known. Although adequate release numbers are essential in birds and mammals, the relationship between number of animals released and the probability of success is thought to be asymptotic in nature, so releasing an overabundance of animals does not necessarily increase success (Griffith et al. 1989).

Quality of the release habitat and the location of this habitat within the historic range of the species (Griffith et al. 1989; Dodd & Seigel 1991) are also important factors for translocation success. If the release habitat is not of high quality, then the chances of a positive outcome are low even when all other factors are taken into consideration. Although we could not evaluate habitat quality in the publications we reviewed, poor or unsuitable habitat was one of the most often reported reasons for translocation failure.

The causes of decline must be addressed prior to the translocation of amphibians and reptiles (Dodd & Seigel 1991). For many amphibian species, this means taking action against *Batrachochytrium dendrobatidis* (the amphibian chytrid fungus) because it can cause the often fatal chytridiomycosis disease. All necessary precautions should be taken to avoid further spread of the disease through human-mediated movement of animals, and release areas for amphibians susceptible to the fungus should be amphibian-chytrid free. Any amphibian release area should also be sufficiently distant from infected areas because the amphibian-chytrid fungus spreads at a rate of up to 120–160 km/year in Australia and 28–42 km/year in Central America (Lips 1998; Alexander & Eischeid 2001; Lips et al. 2006). Recently, a few failed translocations have been traced back to chytridiomycosis, and the amphibian-chytrid fungus has been found in released toads (Fellers et al. 2007; Fisher & Garner 2007).

Future Research and Recommendations for Amphibian and Reptile Translocations

Stress affects translocated animals (Moore et al. 1991; Coddington & Cree 1995; Mathies et al. 2001; Lance et al. 2004; Alberts 2007; Teixeira et al. 2007), and even short holding periods can cause significant acute stress responses, which may exist for up to a month after release (Alberts 2007) in herpetofauna (Moore et al. 1991; Tyrrell & Cree 1998; Lance et al. 2004). A number of researchers have examined the effects of stress from capture, but few have looked at the effects of stress in herpetofauna after release into a new environment. It must be considered that individuals undergoing translocation face several stressors, including capture, captivity, and transportation, that may cause a larger "distress" effect in individuals (Platenberg & Griffiths 1999; Teixeira et al. 2007).

Released animals may be more likely to settle near release sites when they are provided with natal cues that are linked to positive experiences at an earlier life stage (Stamps & Swaisgood 2007). With this in mind, future researchers should investigate soft releases (which allow the animals a period to acclimate to their new environment [Griffith et al. 1989]), resource provisioning, and other such supportive measures to determine whether they increase the success rates of translocations. Little work has been done with natal-habitat preference or soft releases as they apply to herpetofaunal translocations, but there are a few cases that show they can increase site fidelity and translocation success for reptiles (Tuberville et al. 2005; Alberts 2007).

Although there are far fewer studies on the outcomes and effects of amphibian and reptile restocking or augmentation, such techniques may be useful for restoring genetic diversity in inbred populations or improving population recovery (Madsen et al. 1999; Muñoz & Thorbjarnarson 2000; Wilson et al. 2004).

Although the success rate of amphibian and reptile translocations has increased, further improvements are needed. More research is necessary on techniques such as soft release, on how to improve site fidelity, and on short-distance translocation and fencing off problem animals. Translocation projects should never be undertaken without thorough consideration of the ecological implications they may have on the source population, the individuals being released, and the ecosystem into which they are reintroduced. In addition, it is critical that a commitment be made to monitor the reintroduced populations over the short and long term and that these results be made available to the general public regardless of outcome through a centralized database. Without the publication of both successful and unsuccessful projects and the details involved, it is impossible for wildlife managers and scientists to make informed decisions for the future translocations of species.

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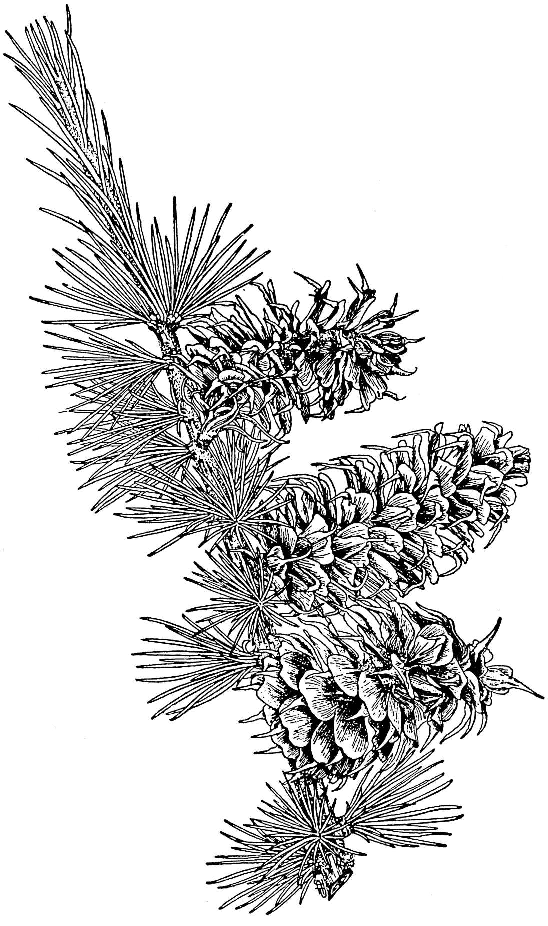

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ORIGINAL PAPER

Spatially explicit decision support for selecting translocation areas for Mojave desert tortoises

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Abstract Spatially explicit decision support systems are assuming an increasing role in natural resource and conservation management. In order for these systems to be successful, however, they must address real-world management problems with input from both the scientific and management communities. The National Training Center at Fort Irwin, California, has expanded its training area, encroaching U.S. Fish and Wildlife Service critical habitat set aside for the Mojave desert tortoise (*Gopherus agassizii*), a federally threatened species. Of all the mitigation measures proposed to offset expansion, the most challenging to implement was the selection of areas most feasible for tortoise translocation. We developed an objective, open, scientifically defensible spatially explicit decision support system to evaluate translocation potential within the Western Mojave Recovery Unit for tortoise populations under imminent threat from military expansion. Using up to a total of 10 biological, anthropogenic, and/or logistical criteria, seven alternative translocation scenarios were developed. The final translocation model was a consensus model between the seven scenarios. Within the final model, six potential translocation areas were identified.

Keywords Conservation and management · DSS · Geographic Information Systems · GIS · *Gopherus agassizii* · Mitigation · National Training Center at Fort Irwin · Threatened species

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Introduction

Decision support systems play an increasing role in natural resource and ecosystem management (Leung 1997) including forest management practices (Rauscher 1999; see recent special issues in Forest Ecology and Management 207:2005 and Computers and Electronics in Agriculture 49:2005), coral reef development (Meesters et al. 1998), aquatic and riparian conservation planning (Reeves et al. 2006), road system analysis in national forests (Girvetz and Shilling 2003), sustainable agriculture (Riordan and Barker 2003), and prioritization of sites for restoration planning in a variety of habitats (Llewellyn et al. 1996; Twedt et al. 2006). The increasing popularity of decision support systems in natural resource and ecosystem management stems from (1) the need to balance increasingly complex multiple land use constraints under current management strategies; and (2) the evolution of computer systems designed to utilize data and generate models to solve management problems. While these systems had rudimentary capabilities in the 1970s (Sprague 1986), today's more complex systems incorporate Geographic Information Systems (GIS), multi-criteria analysis, and fuzzy logic, allowing users to systematically explore alternatives and uncertainty in data, resolve conflicts, and access voluminous scientific information. Conflict resolution is possible because costs and benefits can be explored and alternates readily compared. Decision support systems allow all interested parties to participate and share knowledge of details in a systematic, consistent manner. The final products allow prioritization of management decisions based upon costs and feasibility while providing a process open to the scrutiny of all parties involved.

The National Training Center (NTC) at Fort Irwin, California, is a large (2,598 km^2) Department of Defense force-on-force training area. In 2001 the National Defense Authorization Act (Public Law 107–314 2002) added 545 km^2 of new training lands to the NTC. Approximately two-thirds of the expansion encroaches critical habitat designated for the desert tortoise (U.S. Fish and Wildlife Service 1994b) and the Western Mojave Recovery Unit (U.S. Fish and Wildlife Service 1994a) in which tortoise populations face the greatest number of challenges and obstacles to recovery (Tracy et al. 2004). Of all the recommended mitigation measures (U.S. Fish and Wildlife Service 2004), the most challenging to implement is the translocation of an estimated 2,000 desert tortoises from portions of the expansion area.

Esque et al. (2005) stressed the need for development of a scientifically credible process to identify suitable areas for translocation of desert tortoises. Because science and management objectives sometimes differ, alternative scenarios were needed to test assumptions of the relative importance of model criteria and allay concerns about data uncertainty. To this end, we developed an interactive, spatially explicit decision support system designed to communicate ecological concepts and decision implications. The objectives of this research were: (1) develop an objective, open decision support system to rank landscape suitability for translocation based on multiple habitat and conservation criteria; (2) provide a range of scenarios to accommodate differences of opinion, possible alternative management actions, and uncertainty in data or the effect of ecological processes; and (3) use this decision support system to identify optimal translocation sites for some 2,000 desert tortoises under imminent threat of NTC expansion.

Methods

Study area

The area for prospective translocation covered 20,581 km^2 surrounding the National Training Center at Fort Irwin (NTC) in southern California, USA, including three desert tortoise Critical Habitat Units—Fremont-Kramer, Superior-Cronese, and Ord-Rodman (Fig. 1). The study area was subdivided into 2.59 km^2 cells that served as units of analysis. The area of each cell was equivalent to one U.S. Public Land Survey System section, typically referred to in statutory units of 1 mi^2. This unit size was chosen at the request of the decision makers for the purpose of identifying Public Land Survey System sections that could be purchased to fulfill the land acquisition mitigation measure. We scaled all data sets to this cell size.

Technological framework

The criteria, relationships between criteria, and criteria weights used to evaluate the translocation potential of a site were documented in NetWeaver (Saunders et al. 2005). Using fuzzy logic (Zadeh 1968), we parameterized these criteria, assigning them truth values which ranged from −1 to 1, where 1 was considered completely suitable, and −1 completely unsuitable. We then weighted each criterion according to its relative importance

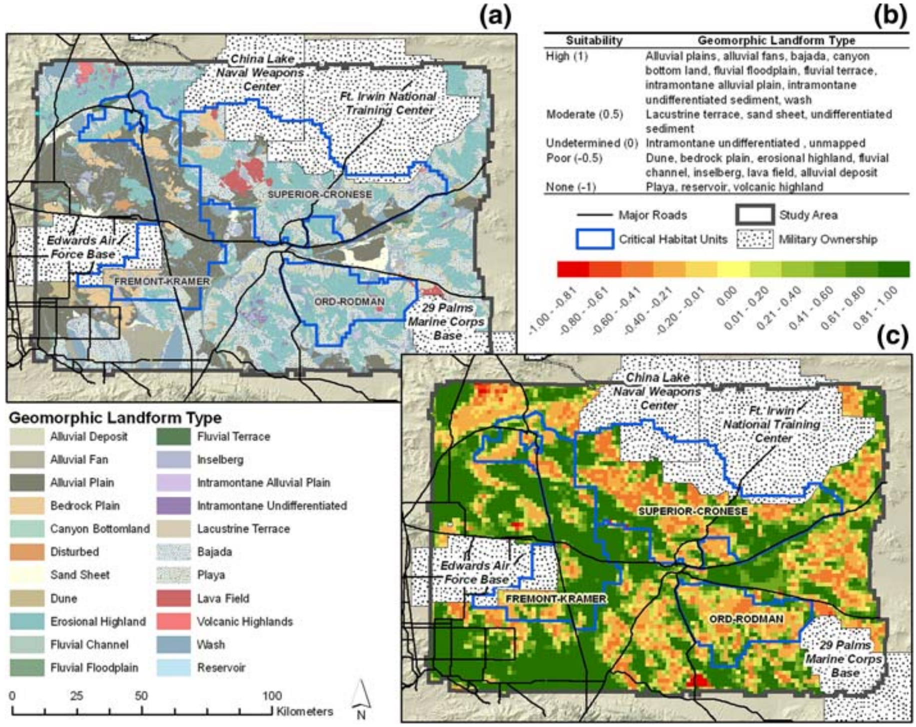


Fig. 1 Habitat criteria. (**a**) Map showing habitat source data, geomorphology. (**b**) Habitat landform model parameters. (**c**) Suitability for translocation based upon habitat. Habitat suitability grades from least suitable (red) to most suitable (green)

based upon expert opinion. The fuzzy logic framework accommodates uncertainty commonly lost in ecological modeling under traditional mathematical models (Openshaw 1996; Reynolds 2001). For example, species distributional limits may be gradual rather than abrupt, or knowledge of these precise limits may be incomplete (Meesters et al. 1998). For every scenario, each section was assigned a truth value related to the degree to which that section was predicted to be suitable for translocation given the combined suitability of all the criteria at that location.

We pre-processed all data for developing the criteria using customized ESRI ArcGIS geoprocessing models. Spatial models for each criterion and all criteria combined were run within the Ecosystem Management Decision Support (Reynolds 2001) ArcGIS extension. Ecosystem Management Decision Support provides a framework for open and spatially explicit decision support modeling in ecological investigations at multiple geographic scales (Reynolds et al. 1996, 2003; Reynolds and Hessburg 2005). The GIS framework allowed us to ask questions of the data and management actions in the form of alternative scenarios.

Model criteria

The criteria selected for prioritizing potential translocation sites included biological and anthropogenic factors affecting desert tortoise populations in the Western Mojave Desert Recovery Unit, as well as logistical constraints. Criteria thought to be important for translocation, along with their model parameters and model weights, were identified in a draft report (Esque et al. 2005). Ten criteria were selected for assessing translocation suitability. Our interpretation of these criteria as good or bad depended on the individual scenario objectives. To start, we developed a base scenario followed by six alternative scenarios. Data sources for the 10 criteria are provided in Table 1 and their suitability for translocation as modeled in the base scenario was as follows.

Ownership

The purchase of private lands within desert tortoise critical habitat was a mitigation measure for expansion. Private lands with many owners are more difficult to purchase than contiguous blocks of land with fewer owners. Because extensive tracts of federal and state lands suitable for translocation existed within the study area, privately held sections were considered less suitable. However, within privately held sections, those with fewer land owners and those surrounded by existing public lands were considered more suitable.

Habitat

Although general knowledge exists as to what constitutes tortoise habitat, no spatial data models support this knowledge other than geomorphology (Fig. 1a), which is believed to play an important role in limiting tortoise distribution and densities (Weinstein 1989; U.S. Fish and Wildlife Service 1994a; Aycrigg et al. 2004). We ranked landforms to reflect their suitability for tortoise habitat (Fig. 1b). Geomorphic suitability was calculated for each section using an area-weighted average of the different landforms contained within that section (Fig. 1c).

Table 1 A total of 10 criteria were considered for assessing desert tortoise translocation suitability. Spatial data in support of criteria were obtained from a number of sources

Criterion	Data source
Ownership	U.S. Bureau of Land Management (California surface land ownership http://www.ca.blm.gov/gis) and supplemented at the section level with parcel and private ownership information provided by the NTC
Habitat	Earth materials mapping project data (http://mojavedata.gov; 2000) and major streams in California (http://www.ca.blm.gov/gis; 1998)
Proximity to major roads and highways	State of California (U.S. Highways in California http://gis.ca.gov; 2002)
Proximity to urban areas	ESRI (U.S. Census Urbanized Areas http://arcdata.esri.com/data/tiger2000/tiger_county.cfm?sfips=06; 2000)
Proximity to projected urban growth	State of California (projected urban growth http://frap.cdf.ca.gov/data/frapgisdata/select.asp 2002)
Road density	State of California (California local roads, California State highways, U.S. Highways in California, Vehicle Trails in California http://gis.ca.gov; 2002) U.S. Bureau of Land Management (route designation west Mojave plan http://www.blm.gov/ca/cdd/wemo.html; 2001)
Critical habitat units	U.S. Fish and Wildlife Service (http://www.fws.gov/nevada/desert_tortoise; 1994)
Off-highway vehicle	U.S. Bureau of Land Management (federal off highway vehicle areas, CA http://www.ca.blm.gov/gis; 1999)
Die-off regions	U.S. Bureau of Land Management Total Corrected Sign tortoise data for 1998, 1999 and 2001 (U.S. Bureau of Land Management West Mojave Plan http://www.blm.gov/ca/cdd/wemo.html; 2001) U.S. Fish and Wildlife Service Line Distance Sampling data 2001–2004 (U.S. Fish and Wildlife Service http://www.fws.gov/nevada/desert_tortoise; 2006)
Proximity to NTC	Provided by the NTC

Proximity to major roads and highways

Tortoises are known to displace up to 15 km after translocation (Berry 1986; Nussear 2004), and evidence of tortoise presence is reduced up to 4 km from major roads (Von Seckendorff Hoff and Marlow 2002; Boarman and Sazaki 2006). Since major roads can be a source of mortality, act as barriers, or at least filter tortoise movement (Gibbs and Shriver 2002; Von Seckendorff Hoff and Marlow 2002), areas <15 km from major roads and highways were considered unsuitable and areas >15 km suitable.

Proximity to urban areas

Urban areas are considered poor habitat; thus, translocation suitability increased with distance from such areas.

Proximity to projected urban growth

Translocating tortoises to areas slated for development (i.e., as part of urban planning and projections) would be counterproductive to recovery goals, posing significant future management challenges. Areas within the projected urban growth footprint were considered unsuitable and those outside suitable.

Road density

Within the Mojave Desert, paved and dirt roads have been implicated in the spread of non-native plant species and increased risk of fire (Brooks 1999; Brooks and Pyke 2001). Moreover, roads are known to negatively impact small mammal, lizard, and tortoise populations and habitat (Busack and Bury 1974; Brattstrom and Bondello 1983; Bury and Luckenbach 2002; Von Seckendorff Hoff and Marlow 2002; Boarman and Sazaki 2006), destroy native biological soil crust important for soil stability (Belnap and Eldridge 2001; Belnap 2002), and facilitate human access (Trombulak and Frissell 2000). Unfortunately, access is accompanied by illegal activities such as releasing captive tortoises, collecting, shooting, harassing, etc. The deleterious effects of the increase in roads on tortoise populations have not been explicitly quantified; however, more roads presumably pose a greater level of threat to tortoises. Road density was calculated as the total km of paved and unpaved roads per section; most roads were unpaved. Areas with more roads were considered less suitable than those with fewer roads (Fig. 2).

Critical habitat

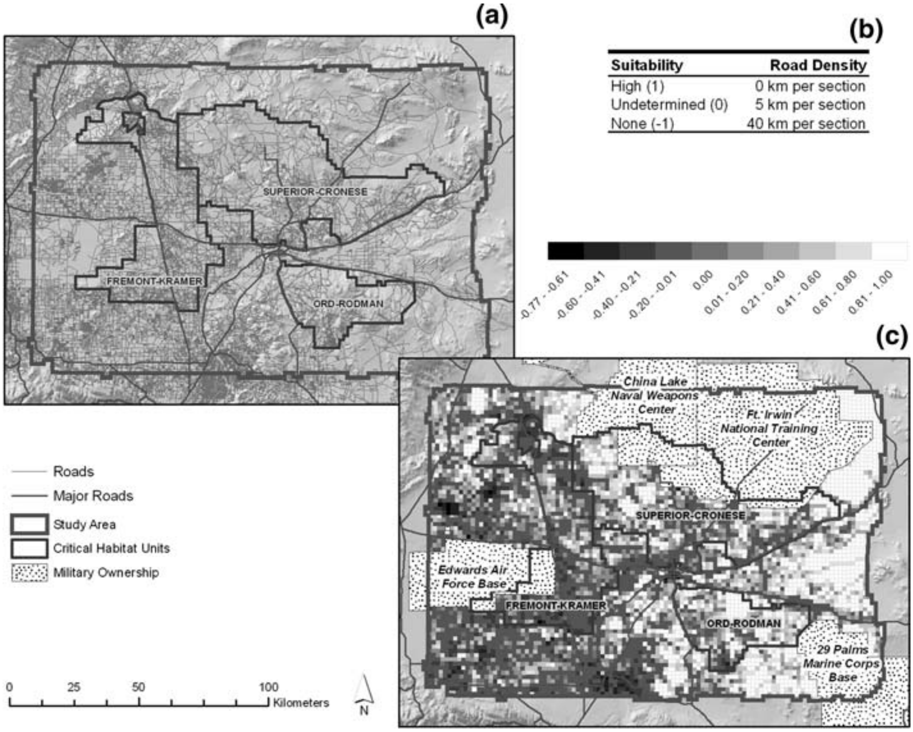
United States Fish and Wildlife Service critical habitat contains physical or biological features considered to be essential to the conservation of a target species (ESA 1973). Areas within desert tortoise critical habitat (U.S. Fish and Wildlife Service 1994b) were considered more suitable than areas outside of critical habitat.

Off highway vehicles

Off highway vehicle activities are detrimental to tortoises by degrading tortoise habitat or crushing tortoises and/or their burrows (Bury and Marlow 1973; Bury and Luckenbach 2002). Therefore, areas designated for open off road vehicle use were considered unsuitable whereas those areas closed to all vehicular traffic or areas where travel was allowed on designated routes only were considered suitable.

Die-off regions

Die-off areas were identified using a custom 2nd order nearest neighborhood analysis of live and carcass observations from U.S. Fish and Wildlife Service monitoring data (2006). A section's die-off score was most influenced by its own score and the score of the eight 1st



Suitability	Road Density
High (1)	0 km per section
Undetermined (0)	5 km per section
None (-1)	40 km per section

Fig. 2 Road density criteria. (**a**) Map showing roads source data. (**b**) Road density model parameters. (**c**) Suitability for translocation based upon road density. Road density grades from most dense (black) to least dense (white)

order neighbors surrounding it. Less influence was given to the 16–2nd order neighbors surrounding the 1st order neighbors. Die-off scores ranged from 0 to 12 (i.e., from no evidence to irrefutable evidence of die-off). With the idea of restocking low density areas or repopulating areas altogether, higher die-off scores were considered more suitable than areas with low die-off scores.

Proximity to NTC

We used proximity to the NTC as a surrogate for actual genetic knowledge. By doing so, we hoped to minimize the disturbance to the population genetics of the resident and translocated populations by giving preference to those areas closer to the NTC. Areas closer to the NTC were deemed more suitable than areas further away.

Factors omitted

Although additional biological and anthropogenic factors potentially affecting tortoise populations were considered, they were not modeled for the following reasons: (1) little or no potential influence in the study area (e.g., latitude and elevation), (2) no suitable spatial data for modeling existed, and efforts required to secure them were time or cost prohibitive (e.g., raven distribution, nutritional composition and distribution of forage, grazing and soil friability), or (3) the spatial resolution of the data were insufficient for detecting meaningful variability (e.g., precipitation).

Relative weighting of criteria

Criteria were arranged in a logical structure and ranked by level of importance for translocation. The criteria were assigned to one of two tiers and weighted by their relative importance for translocation (Fig. 3). The first tier criteria (ownership, habitat, proximity to major roads and highways, and proximity to urban areas), were regarded as the most influential and weighted more heavily, such that if any one of the parameters were unsuitable that section was considered unsuitable for translocation. The second tier criteria were critical habitat designation, the area's off highway vehicle status, proximity to projected urban growth, die-off ranking, road density, and proximity to NTC. Model scores for the second tier criteria were averaged such that no single criterion rendered a section unsuitable for translocation. However, their combined effect could influence the model. All first and second tier criteria were combined to create a translocation suitability value for each section.

Scenarios

Alternative scenarios were generated in the Ecosystem Management Decision Support extension based on changes to a criterion's suitability or its exclusion from the model altogether. For example, in one scenario, critical habitat was ignored, while in another, its suitability was reversed. Although parameterization of each criterion differed among scenarios (Table 2), their structure and weights did not. Alternative scenarios were designed to accommodate (1) possible inaccuracies in the source data, e.g., despite concerns over future projected growth, neither the decision makers nor authors had confidence in the projected urban growth data, (2) scientific and management disagreement regarding parameterization of a criterion, e.g., we disagreed on whether die-off areas would be appropriate translocation sites without knowledge

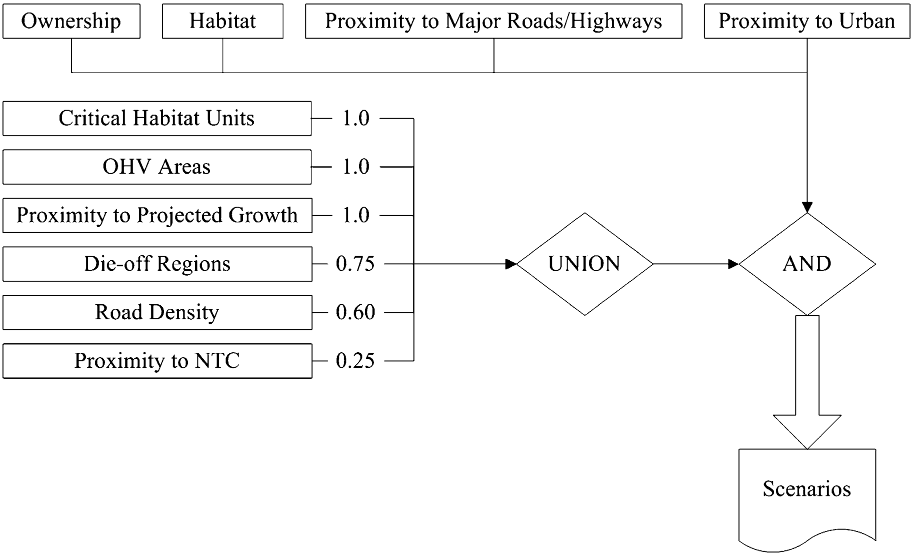


Fig. 3 Criteria model weights used for all scenarios

Table 2 A base scenario and six alternative scenarios were developed for assessing desert tortoise translocation suitability. The base scenario contained 10 criteria. Within the six alternative scenarios certain criterion were either excluded or their suitability for translocation altered from that of the base scenario

	Alternative scenarios						
Criterion	Base	Fence	Ignore proximity to NTC	Fence and ignore proximity to NTC	Ignore critical habitat	Ignore proximity to projected urban growth	Critical habitat and die-off bad
Ownership	X[a]	X	X	X	X	X	X
Habitat	X	X	X	X	X	X	X
Proximity to major roads and highways	X	Proximity not a factor along fenced roads	X	Proximity not a factor along fenced roads	X	X	X
Proximity to urban areas	X	X	X	X	X	X	X
Proximity to projected urban growth	X	X	X	X	X	Criterion excluded	X
Road density	X	X	X	X	X	X	X
Critical habitat units	X	X	X	X	Criterion excluded	X	Criterion reversed from good to bad
Off highway vehicles	X	X	X	X	X	X	X
Die-off regions	X	X	X	X	X	X	Criterion reversed from good to bad
Proximity to NTC	X	X	Criterion excluded	Criterion excluded	X	X	X

[a] An X indicates that the criterion was considered as modeled in the base scenario

of die-off causes, and whether those threats had been alleviated, or (3) alternative future events, e.g., tortoise fencing versus no fencing of areas along major highways.

Base scenario

The base scenario was not assumed to be the preferred scenario, but simply the starting point for discussion. All 10 criteria were included in the base scenario with the state of each criterion identified in Table 2.

Fence scenario

This scenario assumed that tortoise-proof fencing would be installed along portions of Interstate 15, Highway 395, Ft. Irwin Road, and Irwin Road, thus removing the negative effects of these roads from the analysis. This was based on the premise that, all other factors being equal, a fenced road prevents tortoise road kills, whereas a non-fenced road provides tortoises no such protection.

Ignore proximity to the NTC

This scenario ignored proximity to the NTC and thus discounted the argument that tortoises should be translocated the shortest distance from their original residence. At the time this model was produced, the limited genetic information indicated that tortoise populations throughout the west Mojave were genetically similar (Lamb et al. 1989; Lamb and McLuckie 2002; Tracy et al. 2004)

Fence and ignore proximity to the NTC

This scenario combined the fence scenario and the ignore proximity to the NTC scenario.

Ignore critical habitat

This scenario ignored the critical habitat criterion. In other words, this scenario gave no preference for or against critical habitat.

Ignore proximity to projected urban growth

This scenario ignored the projected growth criterion.

Critical habitat and die-off bad scenario

In the original base scenario both critical habitat and die-off areas were ranked as suitable for translocation. Under this scenario, however, we reversed that assumption and assumed both to be bad. While the recovery plan states that up to 10% of any one critical habitat unit could be used for experimental research (U.S. Fish and Wildlife Service 1994a), this recommendation remains controversial, and the scale of this translocation could conceivably encompass more than 10% of the remaining area (post NTC expansion). Placing tortoises in locations where die-offs have occurred without knowing why those deaths occurred is controversial (Frazer 1992). This scenario assessed the relative influence of these concerns.

Results were presented to decision makers in a process designed to be open with respect to methods, tools, and data used to rank criteria suitability and to evaluate scenarios. Hard-copy and digital maps, graphics and tables, interactive models, and 3D visualizations of criteria and scenarios were presented to the group for scrutiny and discussion. No single scenario was considered the best scenario, and all seven were combined to create a consensus model. Sections with suitability values ≥ 0.5 in every scenario represented preferred translocation sites. Sections with suitability values ≤ -0.5 in any one scenario were considered unsuitable for translocation. All other sections were designated as neutral. For example, if a section had a value ≥ 0.5 in six of the scenarios, but a value ≤ -0.5 in the seventh scenario it was considered unsuitable.

Results

A map was produced for each criterion data, the model parameters assigned for that criterion, and the model results (Figs. 1 and 2). Scenarios were presented to decision makers as in the examples in Fig. 4a–c. This process gave the decision makers the opportunity to use the model predictions as objective products for choosing a series of areas suitable for translocation. Seven possible translocation areas were initially chosen and evaluated during site visits. Six were selected as suitable translocation areas (Fig. 5).

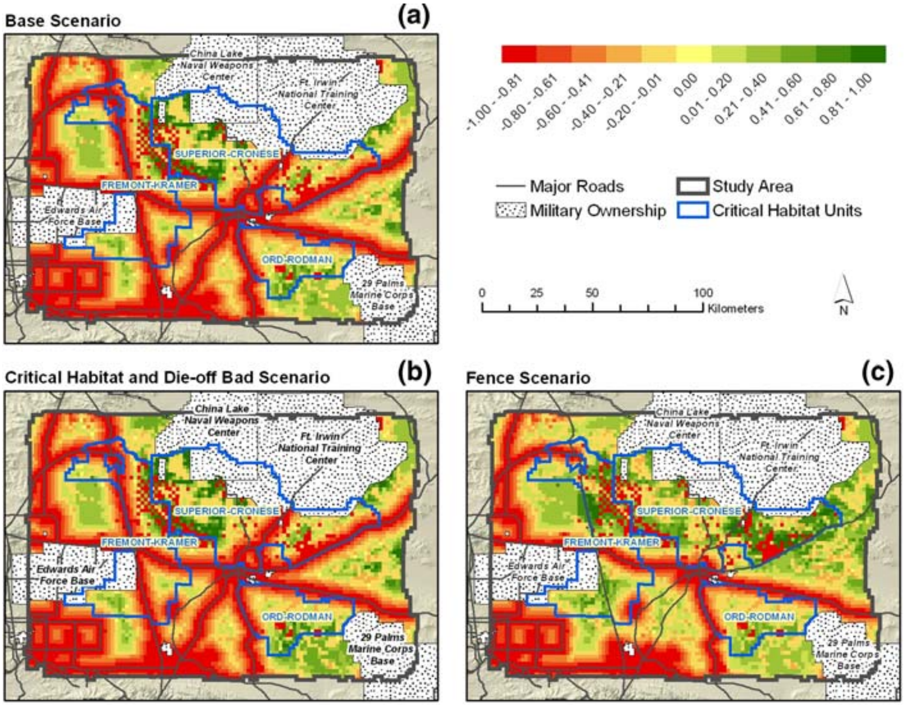


Fig. 4 Graphic of alternative scenarios presented to decision makers. (**a**) Base scenario. (**b**) Critical habitat and die-off bad scenario. (**c**) Fence scenario. The base scenario considers critical habitat and die-off as good and does not factor fenced roads

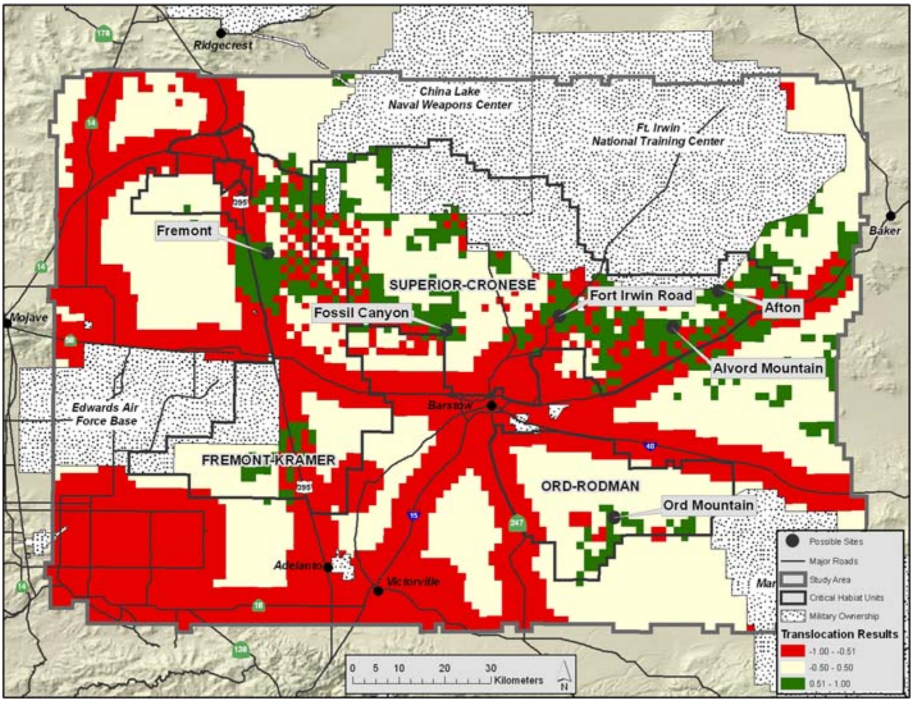


Fig. 5 Final translocation model used for decision making. This map shows the combined common good (green), common bad (red), and common neutral (pale yellow) areas along with the six selected translocation sites

Despite differences of opinion regarding the importance of die-off parameterization (e.g., good versus bad), our modeling outcomes revealed little difference between scenarios relative to the base (Fig. 4a, b). This was due to the greater influence of other criteria, its placement in the second tier of data, and the relative low weight assigned to die-off. This was true for all other scenario comparisons other than fenced roads (Fig. 4a, c). While fencing was never in question as a valid means for preventing tortoise road mortality, this criterion's influence on the model was surprising. Whereas the comparison of the die-off scenarios changed the outcome of only 18 sections, fencing opened up an additional 877 sections as suitable for translocation, a 40% increase in available translocation area.

Discussion

Conservation biologists are often faced with the challenge of assisting with the implementation of decisions based upon not only ecological input, but political and social inputs as well. In the case presented here, all three were considered. The decision to allow expansion was contingent upon the translocation of some 2,000 desert tortoises. We implemented a model using spatially explicit decision support system technologies to foster collaboration between scientists and managers.

Neither the collaboration nor the use of decision support system technologies was easy. For every criterion included in the model there were a dozen that were considered and excluded. There were considerable differences of scientific and personal opinion on how each criterion should be evaluated. Yet these differences were evaluated objectively through scenarios. The technology we used required significant expertise in geospatial technologies. The project succeeded because geospatial, desert tortoise and management expertise were brought together in a collaborative environment. The results of this work (1) provided an objective, open, scientifically credible process that ranked translocation suitability by consensus on habitat and conservation-based criteria, (2) produced seven alternative translocation scenarios from which a single best consensus translocation model was generated, and (3) identified six potential translocation sites.

Objectivity and scientific credibility were achieved in the selection and approval of model criteria using a decision support model based on scientific literature, expert opinion, and peer-review (Esque et al. 2005), with feasibility ultimately vetted by managers. Openness was achieved through the development of alternate scenarios as well as recognition that “conservation is primarily not about biology but about people and the choices they make” (Balmford and Cowling 2006). The consequences of these choices were assessed by modeling alternative scenarios to (1) explore differences of opinion, (2) review consequences of alternative management actions, and (3) explore uncertainty in data.

The process, methods, and tools of the decision support system technologies used in this research integrated key concepts in conservation biology and natural resource management (Kessler and Thomas 2006) and ultimately led to its successful implementation. First, we drew from a wide array of scientific expertise and management perspectives. Second, instead of a theoretical decision support system with no real management application, we addressed an urgent, complex management need that required a practical solution—the translocation of desert tortoises—using the best available scientific information. Third, we addressed this problem by tackling a critical challenge that faces conservation biology today and in the foreseeable future: the development of spatially explicit models for addressing natural resource management needs (Balmford et al. 2005; Balmford and Cowling 2006). Fourth, the process was engaging and used visually compelling and easily understandable graphical formats (Sheppard and Meitner 2005).

Translocation, along with land acquisition, fencing, retirement of grazing allotments, research funding, and route designation and closure, were all identified as mitigation measures to offset the impacts of expansion (U.S. Fish and Wildlife Service 2004). The decision support system developed here could be used for other desert tortoise management and mitigation needs, in particular in the area of additional decision making, adaptive management and/or evaluation of criteria affected by management decisions. This system influenced the decision to fence additional roads. Fencing was originally recommended as a measure to mitigate expansion, but was expected to only occur in a very limited area. As a result of scenario evaluation, its importance was elevated, and extensive fencing is now anticipated along areas of Interstate 15 prior to or in conjunction with translocation. Besides fencing, this system could be used to identify purchasable lands. This could be done by evaluating the number of private owners per section, a logistical factor, the translocation suitability of that section, and the quality of the surrounding lands. In addition, after each land purchase the system could easily be updated and the translocation suitability of each section within the study area recalculated. Because this system is adaptive it could provide real-time updates to translocation suitability and more importantly could lead to what-if land purchase scenarios.

Tortoises will be translocated from the expansion area in two phases. The first phase is expected to included 800 or more individuals. Because this system is adaptive, it could be updated either at the criterion suitability level or scenario level based upon the outcome of the initial translocation. For example, if tortoises in the first phase of translocation move greater than or less than 15 km from their initial release sites, distance from major roads or highways could be adjusted accordingly prior to the second translocation. Third, as new knowledge and data are acquired, especially spatial data, additional criteria can be added or the data supporting a single criterion updated.

Decision support systems, especially spatially explicit ones, are beginning to play an increasing role in natural resources management. However, conservation biologists must be cognizant of the risk of developing decision support systems, for the sake of the scientific exercise, that lack a connection to on-the-ground management needs. Developers of these systems, at least those who intend to affect management, are wasting time and money if their systems are built in the absence of manager and/or stakeholder participation, if appropriate. The system presented here was successful, with success being measured by the degree to which management decisions were based upon the model recommendations, because both scientists and managers invested in the system, and collectively contributed to its design, build and implementation.

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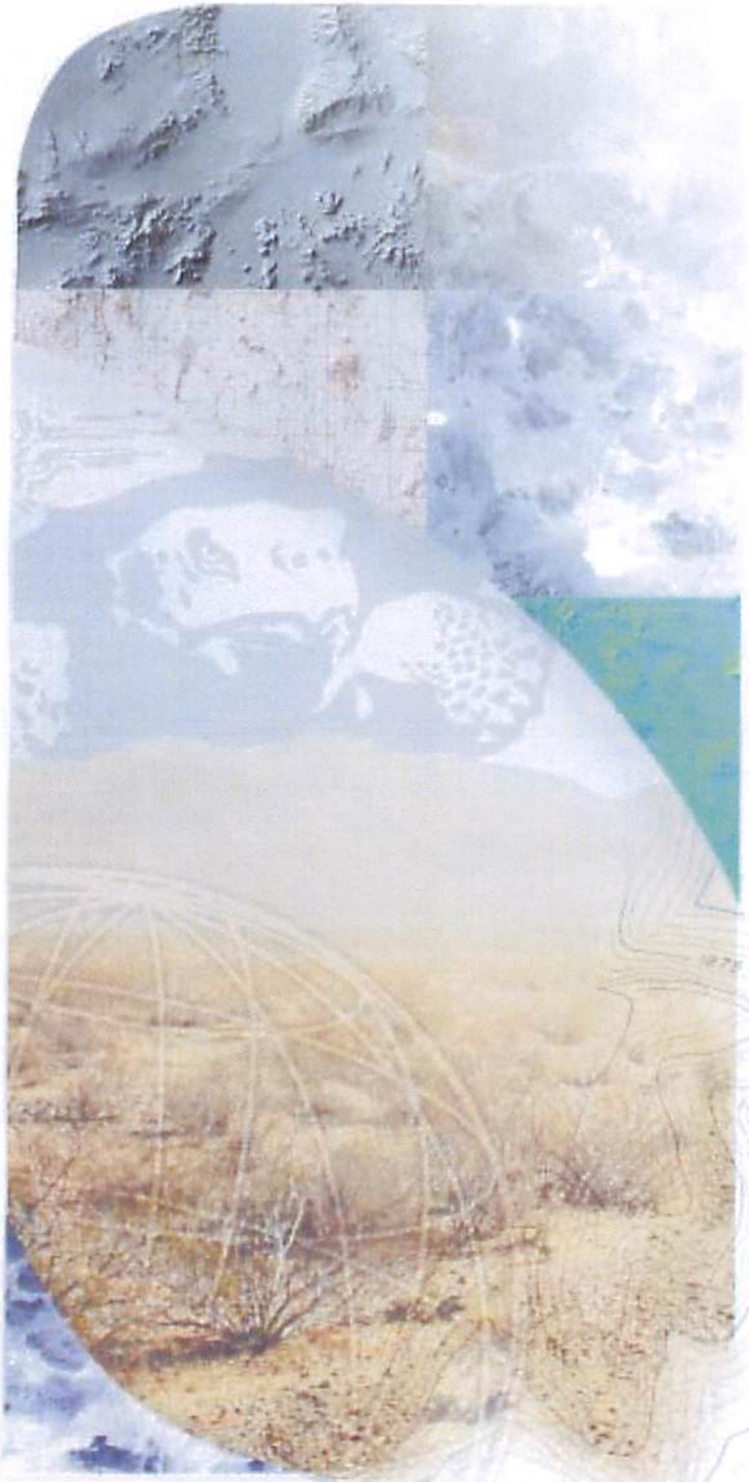
EXHIBIT 459



Habitat Potential Knowledge Base

Redlands Institute Decision Support Team

September 14, 2004
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UNIVERSITY OF
Redlands
THE REDLANDS INSTITUTE

desert
tortoise
PROJECT
UNIVERSITY OF REDLANDS

NetWeaver Model

Elevation Latitude Dynamic Fuzzy Curve Description

Elevation and latitude are modeled together on a dynamic fuzzy curve. The anchor points on a dynamic fuzzy curve change depending on the values on another complementary curve. In this model, the anchor points on the elevation fuzzy curve are dependent on the latitude fuzzy curve. The lower the latitude, the higher the acceptable elevation ranges.

Fuzzy Curve Anchor points, NetWeaver Values, and Descriptions

Table 1 shows the anchor points and values for the elevation fuzzy curve, the latitude fuzzy curve, and how latitude and elevation are calculated together in a dynamic fuzzy curve.

Table 1: Elevation/Latitude Fuzzy Curve Description, Anchor Points, and NetWeaver Values

Description	**Latitude Anchor Point (in decimal degrees)**	**Elevation Anchor Point (in meters)**	**NetWeaver Value**
Moderate elevation at low latitude	33.259	-82.295	*0*
Good elevation at low latitude	33.259	356.76 - 1524	*1*
False elevation at low latitude	33.259	1584.96	*-1*
Moderate elevation at high latitude	37.274	-82.296	*0*
Good elevation at high latitude	37.274	243.84 -1219.2	*1*
False elevation at high latitude	37.274	1280.16	*-1*

Spatial Data Model

Source Datasets and Geoprocessing

Table 2 shows the source data and summarizes the geoprocessing steps used to clip the datasets to the study are and, in the case of latitude, calculate the midpoints for each section in the study area.

Table 2: Latitude and Elevation Source Data and Geoprocessing Steps

Source Data	**Geoprocessing Steps**
Latitude	import PLSS data into Geodatabase use Clip to clip to study area use Spatial Statistics Mean Center to add midpoints to township range section polygons add Latitude field (AS FLOAT) calculate Latitude from midpoint Y field

Source Data	Geoprocessing Steps
Elevation Digital elevation model (DEM) produced in 7.5 by 7.5 minute blocks either from digitized cartographic map contour overlays or from scanned National Aerial Photography Program (NAPP) photographs.	Convert 30 meter DEM raster to vector polygon feature class import into Geodatabase use Clip to clip to study area Union elevation feature class to PLSS Calculate percent of area * elevation Dissolve on unique PLSS Section ID maintaining the sum of the above calculation to obtain area-weighted average of elevation.

Sources of Knowledge

Domain Sources Cited

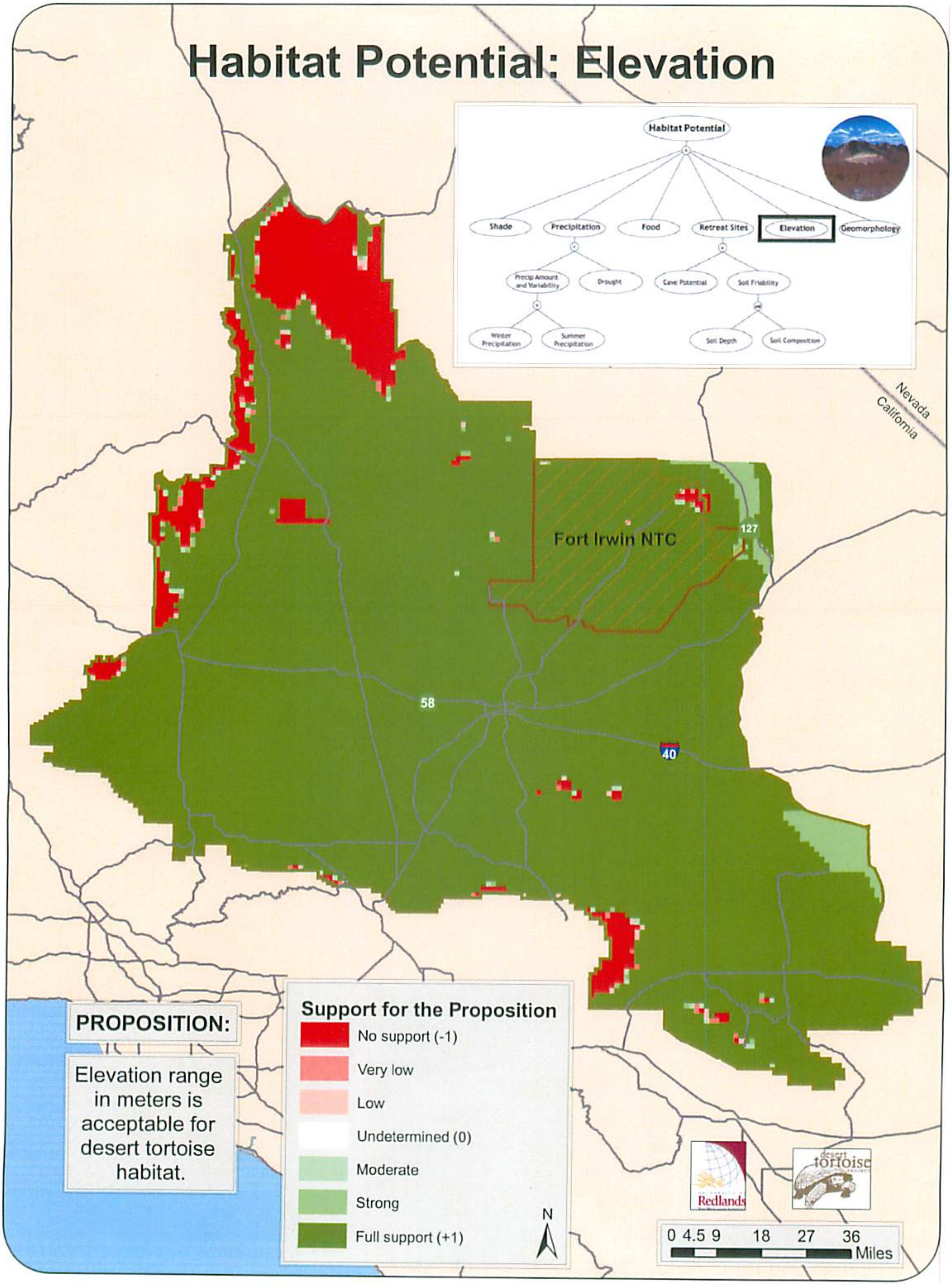
See appendix A for a list of domain experts and notes from the workshops in which they participated.

Richard Tracy, Ph.D.; Director, Biological Resources Research Center; University of Nevada, Reno

Ken Nussear, Ph.D.; U.S. Geological Survey; Las Vegas, Nevada

Phil Medica; Desert Tortoise Coordinator, Southern Nevada Field Office; U.S. Geological Survey

Habitat Potential: Elevation



PROPOSITION:

Elevation range in meters is acceptable for desert tortoise habitat.

Support for the Proposition

- 🟥 No support (-1)
- 🟥 Very low
- 🟥 Low
- ☐ Undetermined (0)
- 🟩 Moderate
- 🟩 Strong
- 🟩 Full support (+1)

Food Resources

Knowledge Model

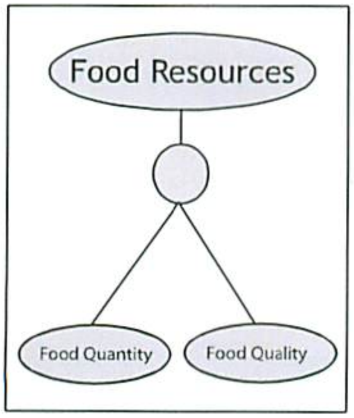
Proposition:

Food resources present are of suitable quality and quantity for a tortoise population.

Explanation:

Desert tortoises are obligate herbivorous reptiles, requiring sufficient food resource quality and quantity. Traditionally, food resources are defined by the quality and quantity of the available vegetation (Oftedal 2002). The 'availability' of vegetation refers to a tortoise's ability to reach, bite, and ingest a piece of plant material.

Figure 1. The Food Resources knowledge model



This model is divided into two primary topics, food quality and food quantity.

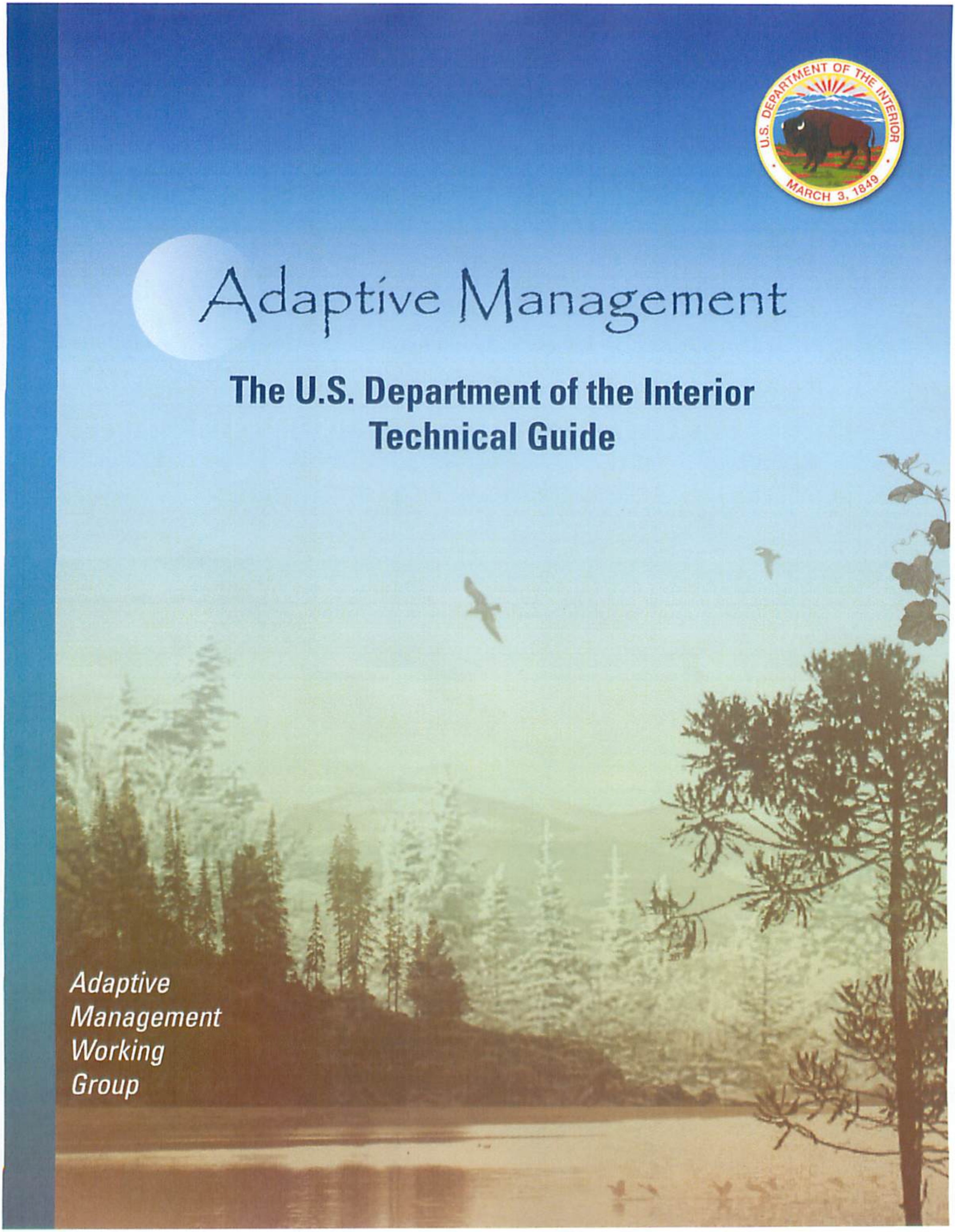
Food Quality

There are several vegetation characteristics that influence the quality of that particular food resource: Water, Nitrogen, Calcium, Copper, Phosphorus, and Protein.

Water

Water is required for basic cellular activities, and is needed in large quantities when metabolizing grasses for digestible nutrients, as well as maintaining electrolyte balance (K,

EXHIBIT 460



MARCH 3, 1849

Adaptive Management

The U.S. Department of the Interior
Technical Guide

*Adaptive
Management
Working
Group*

Adaptive Management

The U.S. Department of the Interior Technical Guide

Adaptive Management Working Group
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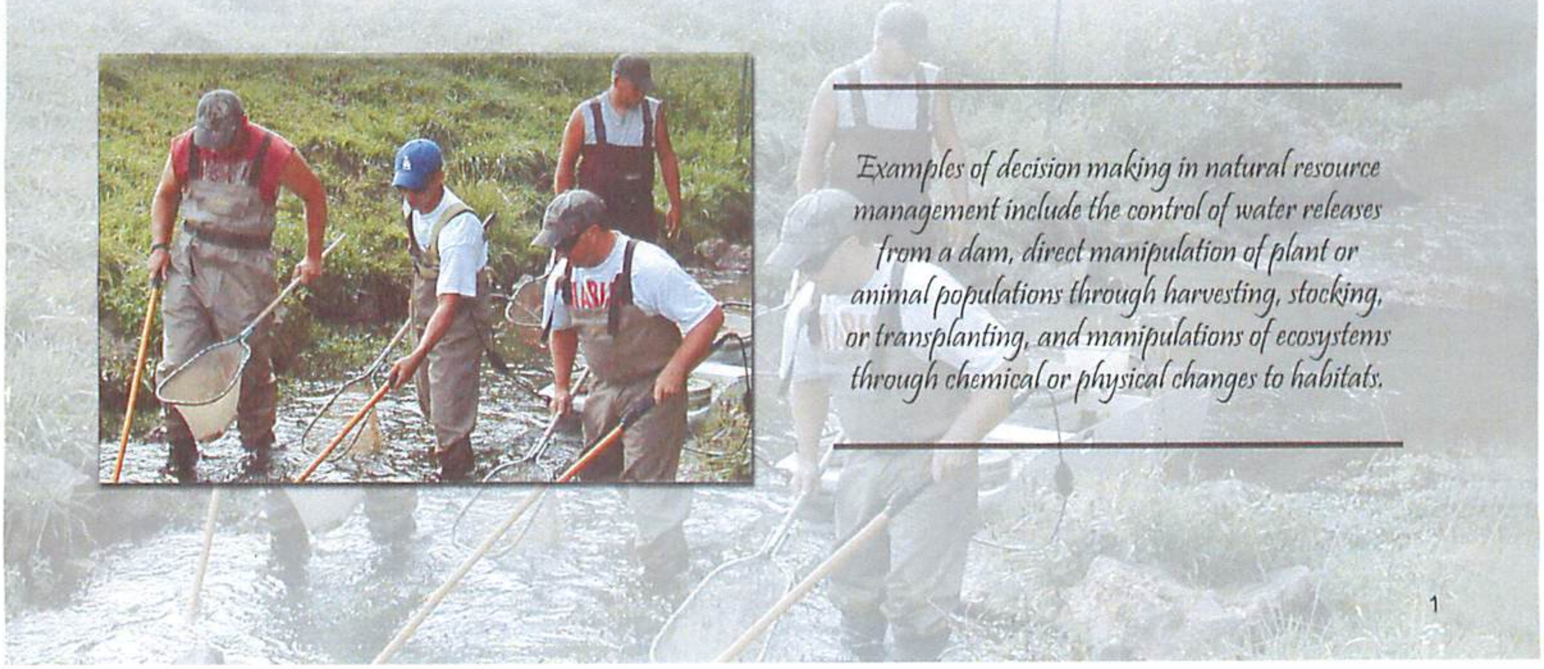
Chapter 1: What is Adaptive Management?

Adaptive management is a systematic approach for improving resource management by learning from management outcomes (1). Its origin can be traced back to ideas of scientific management pioneered by Frederick Taylor in the early 1900s (2,3). Various perspectives on adaptive management are rooted in parallel concepts found in business (total quality management and learning organizations [4]), experimental science (hypothesis testing [5]), systems theory (feedback control [6]), and industrial ecology (7). The concept has attracted attention as a means of linking learning with policy and implementation (8,9). Although the idea of learning from experience and modifying subsequent behavior in light of that experience has long been reported in the literature, the specific idea of adaptive management as a strategy for natural resource management can be traced to the seminal work of Holling (10), Walters (11), and Lee (12).

Adaptive management as described here is infrequently implemented, even though many resource planning documents call for it and numerous resource managers refer to it (13). It is thought by many that merely by monitoring activities and occasionally changing them, one is doing adaptive management. Contrary to this commonly held belief, adaptive management is much more than simply tracking and changing management direction in the face of failed policies, and, in fact, such a tactic could actually be maladaptive (14). An adaptive approach involves exploring alternative ways to meet management objectives, predicting the outcomes of alternatives based on the current state of knowledge, implementing one or more of these alternatives, monitoring to learn about the impacts of management actions, and then using the results to update knowledge and adjust management actions (15). Adaptive management focuses on learning and adapting, through partnerships of managers, scientists, and other stakeholders who learn together how to create and maintain sustainable resource systems (3).

The purpose of this technical guide is to present an operational definition of adaptive management, identify the conditions in which adaptive management should be considered, and describe the process of using adaptive management for managing natural resources. The guide is not an exhaustive discussion of adaptive management, nor does it include detailed specifications for individual projects. However, it should aid both U.S. Department of Interior (DOI) managers and practitioners in determining when and how to apply adaptive management.



Examples of decision making in natural resource management include the control of water releases from a dam, direct manipulation of plant or animal populations through harvesting, stocking, or transplanting, and manipulations of ecosystems through chemical or physical changes to habitats.

1.1. Decision Making and Natural Resource Management

A context for resource management involves a decision making environment characterized by multiple (often competing) management objectives, constrained management authorities and capabilities, dynamic ecological and physical systems, and uncertain responses to management actions. Management thus involves not only predicting how ecological or physical systems are likely to respond to interventions, but also identifying what management options are available, what outcomes are desired, how much risk can be tolerated, and how best to choose among a set of alternative actions. The challenge confronting managers is to make "good" decisions in this complex environment, recognizing that the quality of decision making in the face of uncertainty should be judged by the decision making process as well as progress towards desired outcomes.

A common problem in natural resources management involves a temporal sequence of decisions, in which the best action at each decision point depends on the state of the managed system. Because management actions at each point in time can influence change in the resource system from that time forward, the goal of management is to prescribe objective-driven strategies that account for both the current and future impacts of decisions. A key issue is how best to choose management actions, recognizing that the most appropriate management strategy is obscured by limited understanding.

Often the uncertainty about management impacts is expressed as disagreements among stakeholders who have differing views about the direction and magnitude of resource change in response to management. An adaptive approach explicitly articulates these viewpoints, incorporates them into the decision making process, and uses management itself to help identify the most appropriate view about resource dynamics. In this way, understanding of the resource can be enhanced over time, and management can be improved.

Examples of this kind of decision problem include the control of water releases from a dam, direct manipulation of plant or animal populations through harvesting, stocking, or transplanting, and manipulations of ecosystems through chemical or physical changes to habitats.

The following management issues exemplify sequential decision making in natural resources in the face of uncertainty:

- In a newly established meta-population of wolves, how many animals (if any) should be relocated periodically to maximize the probability that the meta-population will persist over the long term?
- What amount and timing of water release from a dam will maintain downstream water quality, water quantity, and living resources, including people and communities?
- How can an area be managed to minimize the impacts of recreational use on flora and fauna?
- When and how much should water levels be raised or lowered in an impoundment to maximize abundance and availability of invertebrates for foraging shorebirds?
- How can plant communities in an area be managed so as to protect and sustain archeological resources in the area at minimum cost?
- How much forest should be cut each year as part of a pine regeneration program to maximize old-growth pine for use by red-cockaded woodpeckers?
- How can fuel loads be decreased while minimizing effects on forested ecosystems?
- Should annual hunting-season regulations be restrictive or moderate to maximize the longterm cumulative harvest of mallards?
- How much and how often should herbicide be applied to minimize the proliferation of the invasive plant hydrilla in a group of southern lakes?
- In what order should patches of isolated bull trout habitat be reconnected in a network of tributaries to maximize the probability of population persistence while minimizing costs?
- When and where should prescribed burns be used in a collection of management units to maximize the probability that Florida scrub-jays will persist at a refuge over the long term?

Management of problems like these increasingly involves a systems approach with explicit and agreed-upon objectives, management alternatives, and analytical approaches that can identify the most appropriate management strategies. Adaptive management exemplifies such an approach; however, its focus is not only on making good decisions in the present, but also on gaining experience and knowledge so that future management decisions can be improved.

Adaptive management as an example of structured decision making

The move toward accountability and explicitness in natural resource management has led to a growing need for a more structured approach to decision making. Improved clarity about key elements in a decision making process can help decision makers focus attention on what, why, and how actions will be taken. Activities in a structured approach to decision making include the following:

- Engaging the relevant stakeholders in the decision making process
- Identifying the problem to be addressed
- Specifying objectives and tradeoffs that capture the values of stakeholders
- Identifying the range of decision alternatives from which actions are to be selected
- Specifying assumptions about resource structures and functions
- Projecting the consequences of alternative actions
- Identifying key uncertainties
- Measuring risk tolerance for potential consequences of decisions
- Accounting for future impacts of present decisions
- Accounting for legal guidelines and constraints

In the ensuing chapters it will be clear that adaptive management is itself a structured approach to decision making, in that it includes the key elements listed above. The distinguishing features of adaptive management are its emphasis on sequential decision making in the face of uncertainty and the opportunity for improved management as learning about system processes accumulates over time.

Embracing uncertainty

Making a sequence of good management decisions is more difficult in the presence of uncertainty, an inherent and pervasive feature of managing ecological systems (16,17). Uncertainties arise with incomplete control of management actions, errors in measurement and sampling variation, environmental variability, and an incomplete understanding of system dynamics (see Section 5.2). These uncertainties potentially degrade management performance and contribute to acrimony in the decision making process.

Perhaps not surprisingly, managers have sometimes been reluctant to acknowledge uncertainty in environmental assessments and management strategies (18). Often there is a perception that asserting certainty as to management impacts is more convincing, and acknowledging uncertainty increases the likelihood that recommended actions will be ignored. Acknowledgement of uncertain management outcomes is sometimes seen as an invitation for confrontation among different interest groups, resulting in an inability to reach timely agreement on a proposed action.

Adaptive management forces stakeholders to confront unresolved uncertainties that can significantly influence management performance. An adaptive approach provides a framework for making good decisions in the face of critical uncertainties, and a formal process for reducing uncertainties so that management performance can be improved over time.

1.1 Key Points

- Resource management involves decision making in an environment of multiple management objectives, constrained management authorities and capabilities, dynamic resource systems, and uncertain responses to management actions.
- Resource management increasingly involves the articulation of objectives and management options and the use of analytical techniques to identify optimal management strategies.
- Adaptive management is a structured approach to decision making that emphasizes accountability and explicitness in decision making.
- Adaptive management is useful when there is substantial uncertainty regarding the most appropriate strategy for managing natural resources.

1.2. Operational Definition of Adaptive Management

For the U.S. Department of the Interior to effectively implement adaptive management in a consistent and coherent manner across all bureaus, an operational definition is needed that will be applicable for all of DOI. The definition used in this technical guide is adopted from the National Research Council (19):

> Adaptive management [is a decision process that] promotes flexible decision making that can be adjusted in the face of uncertainties as outcomes from management actions and other events become better understood. Careful monitoring of these outcomes both advances scientific understanding and helps adjust policies or operations as part of an iterative learning process. Adaptive management also recognizes the importance of natural variability in contributing to ecological resilience and productivity. It is not a 'trial and error' process, but rather emphasizes learning while doing. Adaptive management does not represent an end in itself, but rather a means to more effective decisions and enhanced benefits. Its true measure is in how well it helps meet environmental, social, and economic goals, increases scientific knowledge, and reduces tensions among stakeholders.

This definition gives special emphasis to uncertainty about management impacts, iterative learning to reduce uncertainty, and improved management as a result of learning. Key points in the definition are discussed in more detail below:

Adaptive management openly acknowledges uncertainty about how ecological systems function and how they respond to management actions (20,21). However, adaptive management is not a random trial-and-error process. Instead, it involves formulating the resource problem, developing conceptual models based on specific assumptions about the structure and function of the resource system, and identifying actions that might be used to resolve the problem. Through the monitoring of outcomes following management interventions, adaptive management promotes improved understanding about which actions work, and why.

Adaptive management is designed to improve understanding of how a system works, so as to achieve management objectives (20,21). Models are used in adaptive management to embed hypotheses about system behaviors and enable managers to predict the impacts of their activities. These predictions are the basis for learning later on. Once activities are implemented, the testing of underlying model assumptions against monitoring data provides the foundation for learning and the improvement of management based on what is learned.

Adaptive management is about taking action pursuant to desired outcomes (21). In adaptive management, the outcomes of decisions, assessed through followup monitoring, are compared against explicit predictions of those outcomes (20), with the comparative results fed back into decision making to produce more effective decision making (11,22,23,24). Actual and expected results can differ for many reasons: underlying assumptions are wrong, actions are poorly executed, environmental conditions have changed, monitoring is inadequate, or some combination of these problems. An adaptive approach helps isolate inadequacies in a management application, allowing adjustments to be made and management to be improved.

Adaptive management requires the participation of stakeholders. Stakeholders include people and organizations who use, influence, and have an interest, or "stake," in a given resource (25). Stakeholders should be involved early in the adaptive management cycle, to help assess the problem and design activities to solve it. Stakeholders also can help to implement and monitor those activities, and participate in the evaluation of results. Involvement of stakeholders from the beginning increases management effectiveness and the likelihood of achieving agreed-upon outcomes (25).

There are many definitions in the literature on adaptive management, but a common theme shared by them all is that adaptive management is a learning-based process (26). The definition used in this guide was chosen because it emphasizes the use of learning to improve management decisions and because it is germane to resource management in DOI.The sequence of activities shown in Fig. 1.1 is often used to characterize adaptive management. Additional structure can be incorporated into this sequence, by recognizing an embedded feedback loop of monitoring, evaluation, and management adjustments that focuses specifically on learning about the impacts of management. Multiple iterations of this loop may occur within each iteration of the overall cycle, accelerating learning about ecological process within the more comprehensive cycle that includes learning about the adaptive process itself (through periodic problem reassessment, design, and implementation). Learning at both levels is discussed in more detail in Section 3.1.

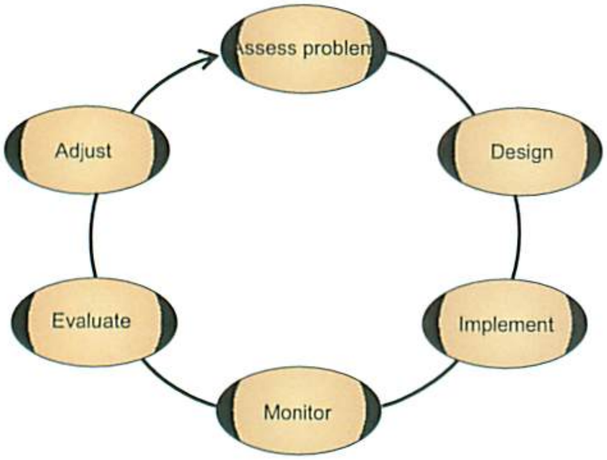
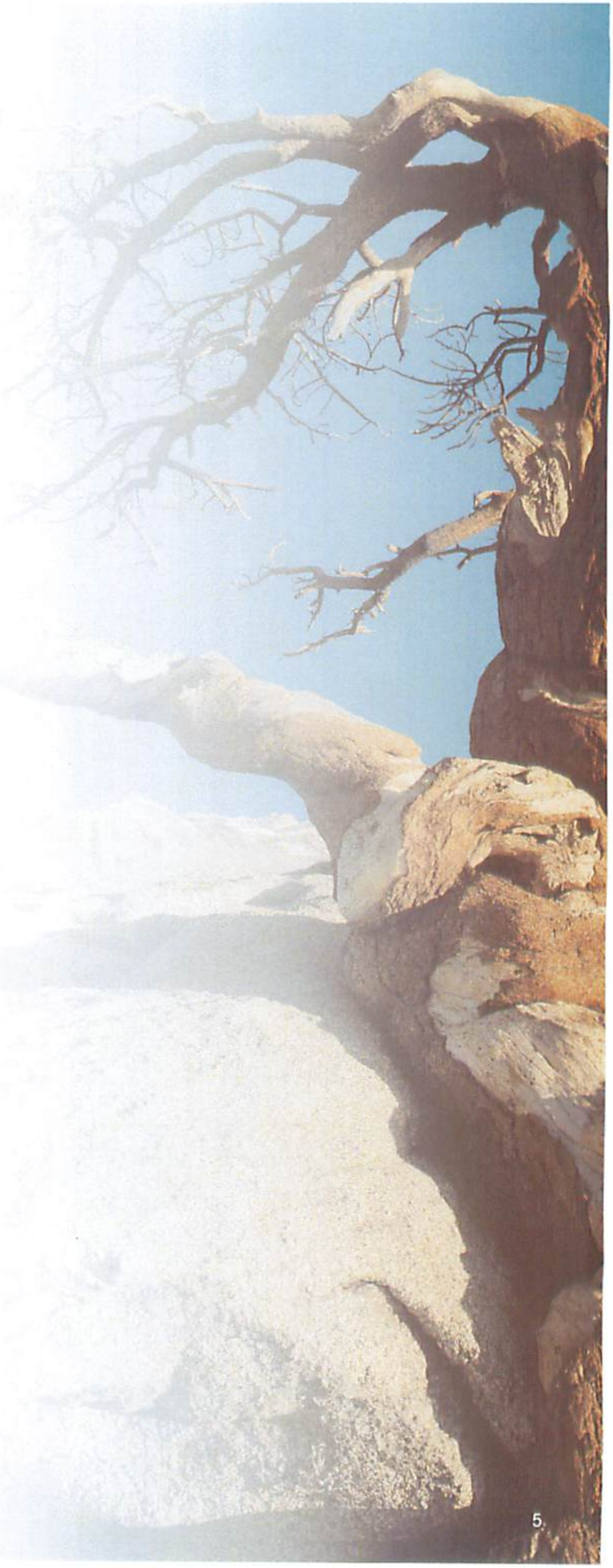


Figure 1.1. Diagram of the adaptive management process.



Other approaches to resource management

Learning from the experience of management is certainly not a new idea, but the purposeful and systematic pursuit of knowledge as an explicit part of management has rarely been practiced. The term "adaptive management" has been used to describe a broad array of approaches that involve learning while doing, but the phrase is not always appropriate. For example, management by trial and error is sometimes described as adaptive management, but at best it is likely to be inefficient, and at worst it can retard the institutionalization of experience and learning. Nor should adaptive management be confused with conflict resolution, which focuses on negotiating tradeoffs among competing interests. Management approaches that primarily depend on expert opinion and advice for decision making are not by themselves adaptive. Finally, in the absence of additional structure in a decision making process, monitoring a managed resource system does not itself make an application adaptive. A great many resource systems are monitored in some manner, but in most cases the resulting data are not used systematically for learning and improvement in a context of objective-driven management.

More formal approaches to decision making can be identified, depending on the amount of uncertainty facing managers and the capacity to influence the system being managed (Fig. 1.2). In an ideal situation in which system controllability is high and management impacts are predictable, formal optimal control approaches can be used to identify optimal management strategies. If one's ability to control the system is limited, hedging strategies or scenario planning can be useful, depending on how well the effects of management can be predicted. As indicated in Fig. 1.2, adaptive management is appropriate if management can strongly influence the system but uncertainty about management impacts is high (27).

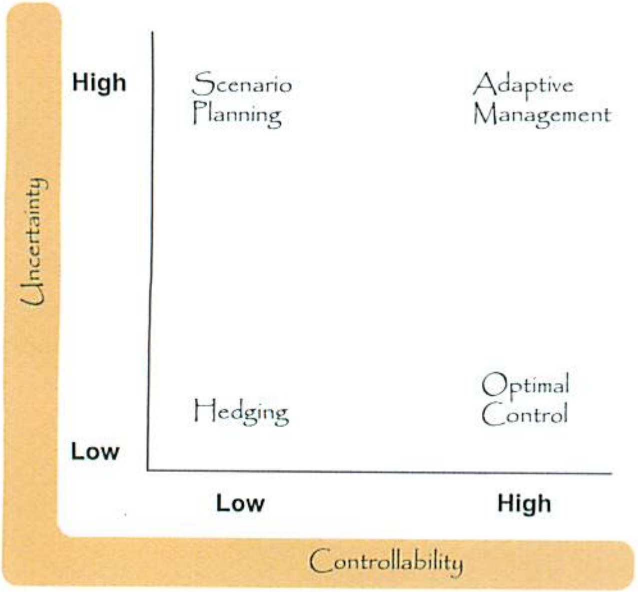
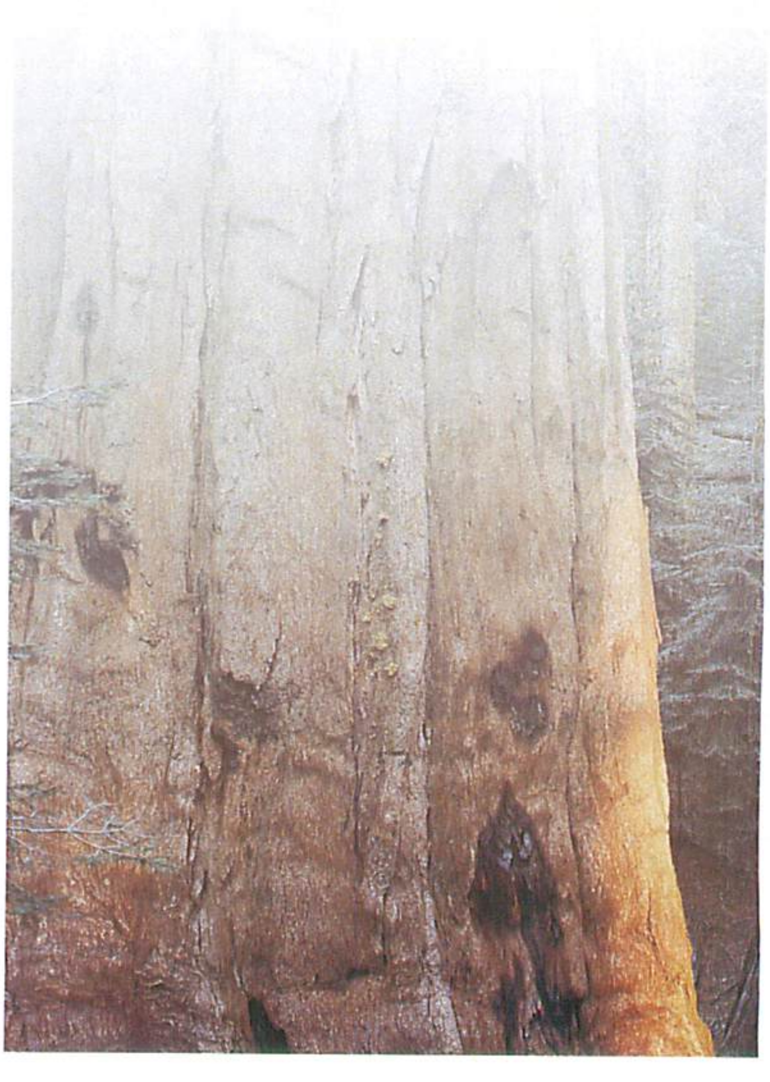


Figure 1.2. Approaches to decision making in a natural resource system. The appropriate approach depends on the influence decisions can have on system behavior and the amount of uncertainty about management impacts (27).



Adaptive management requires stated management objectives to guide decisions about what to try, and explicit assumptions about expected outcomes to compare against actual outcomes. It is important to know what the available management options and alternative assumptions are, in case the action that is tried does not work as expected. The linkages among management objectives, learning about the system, and adjusting direction based on what is learned distinguish adaptive management from a simple trial and error process. In the chapters that follow, we describe adaptive management formally in terms of objectives, management options, and models that embed alternative hypotheses about management responses. But in essence, adaptive management will be seen to be learning by doing, and adapting based on what is learned (28). A comparison of adaptive management with some other approaches to natural resource management is presented in Section 5.1.

1.2 Key Points

- Adaptive management acknowledges uncertainty about how natural resource systems function and how they respond to management actions.
- Adaptive management is designed to improve understanding of how a resource system works, so as to achieve management objectives.
- Adaptive management makes use of management interventions and followup monitoring to promote understanding and improve subsequent decision making.

Adaptive management requires stated management objectives to guide decisions about what actions to take, and explicit assumptions about expected outcomes to compare against actual outcomes.

Calico Solar – 08-AFC-13
DECLARATION OF SERVICE

I, Bonnie Heeley, declare that on August 25, 2010, I served and filed copies of the attached CALIFORNIA UNIONS FOR RELIABLE ENERGY'S EXHIBITS 454 - 460, dated August 25, 2010. 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/calicosolar/CalicoSolar_POS.pdf. The document has been sent to both the other parties in this proceeding as shown on the Proof of Service list and to the Commission's Docket Unit electronically to all email addresses on the Proof of Service list; and by depositing in the U.S. mail at South San Francisco, CA, with first-class postage thereon fully prepaid and addressed as provided on the Proof of Service list to those addresses NOT marked "email preferred."

AND

By sending an original paper copy and one electronic copy, mailed and emailed respectively to:

CALIFORNIA ENERGY COMMISSION
Attn: Docket No. 08-AFC-13
1516 Ninth Street, MS 4
Sacramento, CA 95814-5512
docket@energy.state.us.ca.

I declare under penalty of perjury that the foregoing is true and correct. Executed at South San Francisco, CA, on August 25, 2010

/s/
Bonnie Heeley

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