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STATE OF CALIFORNIA

Energy Resources Conservation
and Development Commission

In the Matter of:

APPLICATION FOR CERTIFICATION
FOR THE (SOLAR MILLENIUM)
RIDGECREST SOLAR POWER
PROJECT

DOCKET NO. 09-AFC-9

INTERVENOR CENTER FOR BIOLOGICAL DIVERSITY'S COMMENTS ON THE STAFF ASSESSMENT

May 21, 2010

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Eric K. Solorio, Project Manager
California Energy Commission
Siting, Transmission and Environmental Protection Division
1516 Ninth Street, MS-15
Sacramento, CA 95814

Dear Mr. Solorio,
Please find the following comment letter on the Ridgecrest Solar Power Project submitted on behalf of the Center for Biological Diversity. References will be included on a CD to be sent with the hardcopy of this letter.

Dated: May 21, 2010

Respectfully submitted,

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CENTER for BIOLOGICAL DIVERSITY
Because life is good.

protecting and restoring natural ecosystems and imperiled species through science, education, policy, and environmental law

May 21, 2010

Eric K. Solorio, Project Manager
California Energy Commission
Siting, Transmission and Environmental Protection Division
1516 Ninth Street, MS-15
Sacramento, CA 95814

RE: Comments on Staff Assessment for the Ridgecrest Solar Power Plant Application for Certification 09-AFC-9, Kern County, March 2010, CEC-700-2010-008 DES-10-14

Dear Mr. Solario,

The Center for Biological Diversity ("Center") is a non-profit environmental organization dedicated to the protection of native species and their habitats through science, policy, and environmental law. The Center has over 255,000 members and online activists throughout California and the United States, including members that live nearby the vicinity of the proposed Ridgecrest Solar Power Plant (RSPP) and recreate there. On April 30, 2010, the Center was granted leave to intervene in this proceeding. The Center submits these comments regarding the March 2010 Staff Assessment ("SA") for the Ridgecrest Solar Power Plant Project ("proposed project") on behalf of our board, staff and members.

I. INTRODUCTION

The development of renewable energy is a critical component of efforts to reduce greenhouse gas emissions, avoid the worst consequences of global warming, and to assist California in meeting emission reductions set by AB 32 and Executive Order S-03-05. The Center strongly supports the development of renewable energy production, and the generation of electricity from solar power, in particular. However, like any project, proposed solar power projects should be thoughtfully planned to minimize impacts to the environment. In particular, renewable energy projects should avoid impacts to sensitive species and habitat, and should be sited in proximity to the areas of electricity end-use in order to reduce the need for extensive new transmission corridors and the efficiency loss associated with extended energy transmission. Only by maintaining the highest environmental standards with regard to local impacts, and effects on species and habitat, can renewable energy production be truly sustainable.

The current site proposed for this project near the town of Ridgecrest California, but the site itself is relatively devoid of human disturbance except for a few dirt roads and the existing Southern California Edison (SCE) transmission lines and associated structures. We concur with the Staff Assessment which states for the biological resources that, "The unique qualities of the site that support high concentrations of DT [desert tortoise] and MGS [Mohave ground squirrel] genetic linkage are irreplaceable and cannot be fully mitigated. Because construction of the

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project would permanently destroy this important biological resource, staff, based on an extensive analysis of the project, cannot recommend that the RSPP be approved." SA at pg.19. Furthermore, we concur with staff that "this site should be protected because of its importance to the DT population and its unique and critical benefits to the MGS" SA at pg. 20.

Because of the significant unmitigatable impacts, the Ridgecrest Solar Power Plant proposal should be denied as proposed. The following comments further address the inadequacies of the project proposal and impacts on biological resources:

II. COMMENTS ON THE DECEMBER 2010 STAFF ASSESSMENT

As stated above, the Center agrees with Staff's recommendation to deny the proposed project, nonetheless, because the Commission continues to consider the proposed project application, the Center offers these comments on the SA.

A. The Alternatives Analysis Outlined in the SA Fails to Comply with CEQA or NEPA

Pursuant to CEQA, the "policy of the state" is that projects with significant environmental impacts may not be approved "if there are feasible alternatives or feasible mitigation measures available which would substantially lessen the significant environmental effects…" Pub. Res. Code § 21002; Guidelines § 15021(a)(2). A proposed project should not be approved if environmentally superior alternatives exist "even if these alternatives would impede to some degree the attainment of the project objectives, or would be more costly." Pub. Res. Code §§ 21002; Guidelines §§ 15021(a)(2), 15126.6. The proposed project must be rejected if an alternative available for consideration would accomplish "most [not all] of the basic objectives of the project and could avoid or substantially lessen one or more of the significant effects." Guidelines § 15126.6(c).

Accordingly, the environmental review documents must consider a range of alternatives that would achieve the basic objectives of the project while avoiding or substantially lessening significant environmental effects, and it is essential that the "EIR shall include sufficient information about each alternative to allow meaningful evaluation, analysis, and comparison with the proposed project." CEQA Guidelines § 15126.6. Alternative sites must also be considered where relocating the project would substantially lessen the significant impacts of the project. Guidelines Section 15126.6(f)(2). *See Citizens of Goleta Valley v County of Santa Barbara* (1988) 197 Cal.App.3d 1167; *Save Round Valley Alliance v. County of Inyo* (2007) 157 Cal.App.4th 1437 (whether an alternative site may be feasible even where it requires a change in land use designation; to determine feasibility requires detailed analysis of the alternatives; and even if an alternative is less profitable than the project as proposed it may still be a feasible alternative).

NEPA similarly requires that a range of meaningful alternatives be explored in the environmental review process. 42 U.S.C. §§ 4332(C)(iii),(E). The agency must "study, develop, and describe appropriate alternatives to recommend courses of action in any proposal which involves unresolved conflicts concerning alternative uses of available resources." 42 U.S.C. § 4332(2)(E). This requirement applies whether the agency undertakes an environmental assessment ("EA") or an environmental impact statement ("EIS"). 42 U.S.C. § 4332(2)(E); *see* 40 C.F.R. §§ 1501.2(c), 1508.9(b). In addition, pursuant to the BLM's CDCA plan, impacts to wildlife from conflicting land uses should be avoided. CDCA Plan at 28. Avoidance can best be accomplished through alternative project siting and/or project design.

We concur with the Energy Commission Staff's alternatives analysis that, based on the alternatives presented, "the No Project/No Action Alternative to be superior to the proposed project." SA at pg.B.2-1. However, the range of alternatives actually analyzed in the SA is quite narrow and the SA should have included and analyzed additional alternatives including off-site alternatives and other alternative technologies for example distributed PV.

While the SA alternatives analysis originally considered 26 different alternatives, only four were selected for inclusion in the alternatives review – no project, proposed project, proposed project north of Brown Road and proposed project south of Brown Road. Because these alternatives fail to include review of alternative sites and technologies, the agency may not have as yet adequately explored a range of alternatives. The SA discusses a private lands alternative that appears to substantially reduce the biological impacts – the Garlock Road Alternative site - and an on-site Photovoltaic Technology/Utility Scale alternative, but it should have also fully explored other alternatives that would achieve the same level of renewable energy production—the basic objective of the project—but without the significant impacts of the proposed project. For example, other alternatives sites on previously disturbed lands closer to areas of consumption should be explored. The added costs and energy losses from transmission may make it more cost effective to locate a solar power generating facility closer to the point of use in the cities such as Los Angeles and San Diego which have significant "solarity". In evaluating this factor the agency should assess whether re-use of disturbed sites near existing population centers could both meet the project objectives and avoid many of the significant environmental impacts of the project including impacts to rare and endangered species. Given the economic set-backs of past years, there are more and more large-scale industrial areas that are under-utilized in many parts of southern and central California. These industrial parks, malls and auto rows long ago replaced native habitat, they are connected to the power grid, and are readily accessible to workers. Converting these areas to solar centers is a feasible alternative that would have many societal benefits (including maintaining robust economic zones and avoiding urban blight) and would avoid nearly all of the environmental impacts of siting this project in intact, occupied, highly functional desert tortoise and Mohave ground squirrel habitat in the Mojave desert. Accordingly, the staff assessment should have also explored the use of distributed smaller-scale solar as an alternative. To the extent that such alternative sites may limit some impacts while increasing efficiency of production through minimization of line loss, they should also be explored as part of a meaningful range of alternatives.

The distributed PV alternative was dismissed from detailed consideration in the SA because "increased deployment of distributed solar photovoltaic technology faces challenges in manufacturing capacity, cost, and policy implementation." While the Center agrees that current policy constraints may disadvantage distributed solar photovoltaic technology, these policies are constantly evolving and distributed PV projects at a "mid-scale" of 20 MW or less are being proposed in many areas as well as aggregated projects with smaller distributed components such as the 500 MW project recently approved by the PUC for Southern California Edison. The other two challenges discussed in the SA are equally applicable to the on-site Photovoltaic Technology/Utility Scale alternative, and therefore are not a basis for dismissal.

The SA basically dismisses all of the alternatives except the no action and three on-site alternatives because "All offsite alternatives are considered unreasonable by the Bureau of Land Management because, … none would accomplish the purpose and need for the proposed action" SA at pg. B.2-2. This statement shows that an unreasonably narrow framing of the objectives was used to develop the viability of alternatives for analysis rather than a proper consideration of the true objectives or purpose and need for the proposed project. The basic objectives of the project are to provide 250-MW of renewable power in California. This goal can be met in a number of ways by feasible alternatives that would avoid impacts to the desert tortoise and intact habitat, Mohave ground squirrel, its habitat and its connectivity, water resources, and waters of the state.

The agency is charged with considering alternatives to avoid and minimize impacts, it cannot lawfully fulfill this duty based on the limited alternatives analysis presented in the SA.

B. Additional Analysis is Needed to Assess All Impacts that Require Avoidance and Minimization

Some impacts that were not fully analyzed in the SA as follows:

Incomplete surveys: Because the proposed project boundaries are in flux, additional biological surveys are being completed to survey areas previously not surveyed as well as to supplement previous surveys (SA at C.2-5, C.2-9, C.2-28-29, C.2-32, C.2-34, C.2-37). That additional information needs to be included in a supplemental SA in order for decision-makers and the public to have access to information regarding the existing conditions of the actual proposed project and the public should be given an opportunity to respond to the new information.

According to the SA, only a single day (May 2, 2009) survey was done over the whole project site for some rare plants (C.2-16-17). This effort is insufficient to comprehensively survey the proposed project site.

Growth-Inducing Impacts: CEQA requires environmental analysis to consider the ways in which the proposed project could foster economic, housing, or population growth, whether directly or indirectly in the surrounding environment. Guidelines § 15126.2(d); *see also* 14 Cal. Code Regs § 15358(a)(1) ("Indirect or secondary effects may include growth-inducing effects and other effects related to induced changes in the pattern of land use, population density, or growth rate, and related effects on air and water and other natural systems, including ecosystems."). The Guidelines specifically require that the EIR should "discuss the characteristics of [] projects which may encourage and facilitate other activities that could significantly affect the environment, either individually or cumulatively." Guidelines §

15126.2(d). Growth-inducing impacts from the proposed RSPP project in the Indian Wells Valley include encouraging additional large-scale solar projects to be sited in this same area and making it more likely that additional solar development projects could be approved in this same area. For example, the placement of one industrial project and new access roads may make it more likely that a second or third project will be sited in this area. Siting multiple projects in this area could lead to significant impacts to the listed species in the area due to a severe loss of habitat values in the valley from both habitat loss and fragmentation. This would be a significant change to an area which now contains occupied, essential, contiguous, high value, intact habitat for the desert tortoise, Mohave ground squirrel and other species. The two paragraph growth-inducing analysis (SA at pg. A-9) fails to adequately identify growth inducing impacts and assess them.

Fire Risk: The RSPP project is a solar thermal power plant, which is comprised of fields of mirrors focusing solar energy on tubes of that superheat fluids. The superheated liquids are a fire threat, particularly if flammable materials, like vegetation, are located nearby. Neither the Worker Safety and Fire Protection Section or the Biological Resources Section identify the potential impact to the adjacent habitat from fire originating on the site. Fire in desert ecosystems is well documented to cause catastrophic landscape scale changes[1] and impacts to the local species[2]. Based on the valuable habitat adjacent to the projects site, habitat that would indeed become a refugia for many of the species currently found on site, recognition and evaluation of impacts from a "wildfire" needs to be included.

C. Desert Tortoise

The desert tortoise is continuing to decline throughout its range[3] despite being under federal and state Endangered Species Acts protection as threatened. The SA provides an excellent review of the existing conditions and impact analysis from the project. As stated, the Center agrees with the SA that the impacts to desert tortoise from the project are significant and unmitigable and that the project should be denied.

However, the SA goes onto propose potential mitigation measures that could be put in place if the proposed project was approved; these comments address those proposed mitigation measures. Relocation/translocation is proposed to move desert tortoise out of harms way, if the project was to move forward. As experts explained at the workshop on May 3, 2010, translocation results in significant losses of animals (K. Berry), where to date only 41% of a subset of monitored translocated desert tortoises have survived since being moved in the spring of 2008 as part of the Fort Irwin translocation effort. The Scientific Advisory Committee of the U.S. Fish and Wildlife Service's Desert Tortoise Recovery Office has concluded that

> "translocation is fraught with long-term uncertainties, notwithstanding recent research showing short-term successes, and should not be considered lightly as a

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[1] Brown and Minnich 1986, Lovich and Bainbridge 1999, Brooks 2000, Brooks and Draper 2006, Brooks and Minnich 2007

[2] Ducher 2009

[3] USFWS 2009

> management option. When considered, translocation should be part of a strategic population augmentation program, targeted toward depleted populations in areas containing "good" habitat. The SAC recognizes that quantitative measures of habitat quality relative to desert tortoise demographics or population status currently do not exist, and a specific measure of "depleted" (e.g., ratio of dead to live tortoises in surveys of the potential translocation area) was not identified. Augmentations may also be useful to increase less depleted populations if the goal is to obtain a better demographic structure for long-term population persistence. Therefore, any translocations should be accompanied by specific monitoring or research to study the effectiveness or success of the translocation relative to changes in land use, management, or environmental condition." [4]

. Translocation may be appropriate as a tool to augment populations within depleted recovery units. While it maybe an impact minimization strategy it is not a successful mitigation strategy.

The Western Recovery Unit for the desert tortoise is the largest and most heterogeneous unit.[5] Recent genetics investigations indentified three unique genotypes occurring within the Western Mojave Recovery Unit.[6] In 1994, the Western Mojave unit was the only recovery unit that showed a statistically significant downward trend in population.[7] The latest data from FWS on the trend in population shows an additional 23% decrease between 2005 and 2007 in the West Mojave Recovery Unit (as well as decreases in every other recovery unit).[8] We also note that the project site lies in the same recovery unit as the ill-fated Fort Irwin desert tortoise translocation referenced above, which is also causing continuing additional significant mortality since 2008. The proposed project site supports a robust density of desert tortoises with good population age distribution that is actively reproducing in a genetically unique area of the Western Mojave Recovery Unit, whose general population has been on the decline for decades and continues to do so. In other words, the proposed project site is a success story for a species that is otherwise slipping closer to extinction.

Currently, it is our understanding that additional spring surveys are being undertaken for desert tortoise on the project expansion areas to the north of the original project footprint. It is unknown how many tortoise currently reside on the project site. No relocation/translocation plan has been provided for public review and recipient relocation/translocation areas have not been identified. Clearly site selection and the alternatives analysis comes into play here - selecting a better site for project implementation that is not in desert tortoise habitat or that is in lower quality habitat would eliminate the need for expensive and to-date unsuccessful relocation/translocation.

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[4] http://www.fws.gov/Nevada/desert_tortoise/documents/sac/20090313_SAC_meeting_summary.pdf

[5] FWS 1994

[6] Murphy et al. 2007

[7] FWS 1994

8 FWS 2009

When a Relocation/Translocation plan is developed for the project all recommendations in the Desert Tortoise Recovery Plan[9] regarding relocation/translocation should be incorporated into that document and it should be circulated for public review and comment.

In addition to the avoidance and minimization measures and translocation efforts, adequate mitigation at a rate of at least 5:1 to off-set the impacts to this unique location and high quality habitat for desert tortoise is required. In order to accurately mitigate for the unique desert tortoise population that will be affected by the proposed project, the mitigation needs to occur as close to the proposed project site as possible and before or simultaneously with project site development—mitigation should not lag behind development. Moreover, any mitigation/translocation/relocation sites need to be protected from other threats to the tortoise including future development, roads, and grazing and must be preserved in perpetuity. As staff is already aware, previous mitigation sites are now being proposed for renewable energy projects (CEC-700-2010-009-SA-DEIS [Calico] at pg. C.2-3) – essentially mooting the point of mitigation in perpetuity. Similarly, renewable energy projects have been proposed on lands that were donated to the BLM for conservation undermining the intent of the donors.

D. Mohave Ground Squirrel

The SA provides a good review of the existing conditions on the site and impact analysis from the proposed project, based on the proponent's agreement to recognize the site as occupied habitat for the Mohave ground squirrel (MGS) in order to avoid the expense and effort needed for appropriate surveys. As stated above, we agree with the SA that the impacts to the MGS from the project are significant and unmitigable and that the project should be denied. Connectivity is key to recovering MGS populations through their limited historic range. Further fragmentation of their habitat will increase isolation of existing populations. Conservation of the existing corridor between the Dixie Wash and Edwards Air Force Base along Highway 395, which includes the proposed project site, is recommended as an essential conservation strategy.[10] In particular, the loss or restriction of movement corridors for MGS on this site could have long-term impacts to MGS survival and recovery.

As with the desert tortoise, these comments address the mitigations proposed in the SA. As discussed at the workshop on May 4, 2010, translocation/relocation of MGS is an experimental technique that is not a proven success. (P. Leitner). Recognizing that trapping and relocation is proposed as an avoidance measure, it is still unclear how successful this avoidance measure will be since there is currently no estimate of MGS density on the projects site (because no surveys were undertaken). However, the fact that 77% of the project site is considered medium to high quality habitat (SA at pg. 3.2-34), is evidence that the numbers of MGS individuals affected could be quite high. Clearly trapping and relocation would need to take place at an appropriate time of year when the MGS are most active and again when the young are dispersing.

E. Other Rare Species

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[9] FWS 1994

[10] Leitner 2008

We remain concerned about the evaluation of impacts to the burrowing owl. Burrowing owls are not evenly distributed across the California deserts. The seven active burrows, at least one with juveniles and an additional four individuals (SA at pg. C.2-32) appears to represent a substantial number of burrowing owls for the northern Mojave desert area. Preliminary results from the 2006-7 statewide census identified very few burrowing owl pairs in the northern Mojave desert - only one pair out of 64 survey blocks.[11] The SA fails to evaluate the potential impact of the proposed project on the northern Mojave regional distribution of owls.

While "passive relocation" does minimize immediate direct take of burrowing owls, ultimately the burrowing owls' available habitat is reduced, and "relocated" birds are forced to compete for resources with other resident burrowing owls and may be moved into less suitable habitat.

Additional survey information on golden eagle usage of the site needs to be included. While golden eagles are likely to use the site (SA at pg. C.2-26), it is unclear how close current nest sites are to the proposed project site and if/how golden eagles use the site for foraging, especially while rearing chicks, when foraging areas are reduced in size.[12] Golden eagles have also been documented to avoid industrialized areas that are developed in their territory.[13] Because of the density of golden eagles in the general area, the SA needs to analyze the displacement of on-site territory. Decreasing the foraging area for golden eagles will likely result in a decrease in the number of eagles that can be supported by the remaining habitat.

As discussed at the workshop, cooling ponds are now being proposed on the project site—a significant change in the project description that was not addressed in the SA. Surface water in the desert is a magnet for wildlife and, therefore, a supplemental SA will be needed to address this issue as well as others. The supplemental SA must clearly identify the change in the project and analyze the impacts to wildlife including but not limited to migratory and resident birds and bats.

F. Water Resources

Because water is such a rare resource in California's deserts and is being depleted by both development and changes in rainfall patterns, its availability is of concern for wildlife resources, especially groundwater overdraft. The mitigation options (SA at pg. C.9-28), that the staff has asserted are feasible, are in fact questionable. For example, "Water Supply through the LADWP" - no firm commitment is presented that LADWP would be interested or able to supply water to offset the groundwater pumping. The "cash for grass" xeriscaping of residential and commercial landscaped areas, appears to be a voluntary program and therefore can not be relied upon to mitigate for groundwater pumping. The same concern is true of the only other proposed mitigation – fallowing of agricultural land within the basin – relinquishment of water use for such programs is voluntary. In sum, the SA does not show that mitigation is feasible for the likely impacts of the proposed project's projected water use.

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[11] IBP 2008.

[12] Marzluff et al. 1997

[13] Walker et al. 2005

Waters of the State: The SA indicates that the number of acres of Waters of the State that would be impacted by the proposed project are unknown (SA at pg. C.2-57). The impacts to streambeds and washes which are a critical component of this desert habitat must be fully evaluated. Again, the lack of information and evaluation indicates that the SA is incomplete and a supplemental SA that includes these and other important data must be prepared and circulated for public review.

G. Cumulative Impacts are Not Fully Disclosed and Analyzed

CEQA requires not only full disclosure of cumulative impacts but a full and fair effort on the part of the agency to first avoid such impacts, and then to ensure any remaining impacts are minimized and mitigated. While we agree with the staff conclusions that not all cumulative impacts can be mitigated, the SA suffers from a lack of adequate identification and analysis of these issues.

The cumulative impacts section needs to be updated to include additional projects that are currently going through CEQA review in the general are of the RSPP. Several projects are proposed in Kern County on undisturbed private lands that are not included in the cumulative analysis list including Mojave Solar (both the Barren Ridge project and the Cal City project), the Ridge Rider project and the Weldon solar projects[14]. In San Bernardino County, the Lightsource project near Kramer junction is also proposed on undisturbed private lands where desert tortoises occur[15]. Clearly there could be additional impacts to the desert tortoise, MGS and other rare species, as well as to water resources and other resources from these projects and all of these impacts need to be evaluated in a supplemental SA.

One focus for the cumulative impacts is to look at projects and other impacts (off-road vehicles impacts for example) within the confines of the western Mojave desert, and the cumulative impact on the western Mojave Recovery Unit for the desert tortoise, which as stated above is continuing to decline.

Additionally, the cumulative impacts need to identify the impacts to desert tortoise and MGS and other rare species that may occur due to translocation/relocation efforts associated with the cumulative projects. As the other potential projects get implemented, it will push higher and higher numbers of desert tortoises and other species into smaller and smaller areas and more fragmented habitat.

III. CONCLUSION

For this and future proposed projects, mechanisms should be put in place that encourage solar facilities to be sited on disturbed lands instead of in fully ecologically functioning occupied habitat such as is found on the RSPP site, which supports a variety of rare and threatened species.

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[14] http://www.co.kern.ca.us/planning/noticeprep.asp

[15] http://www.co.san-bernardino.ca.us/landuseservices/Public%20Notices/Projects/Projects.htm

We hope and expect that the Commission will carefully consider all meaningful alternatives and go beyond the admittedly “preliminary” information provided in the SA. The agency should revisit these issues in detail and provide a full range of alternatives as part of a supplemental SA for public review.

Thank you for the opportunity to submit these comments, and we look forward to participating in the process as it moves forward. Please feel free to contact me for additional information at 323-654-5943 or at ianderson@biologicaldiversity.org

Best regards,

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SPATIAL USE AND HABITAT SELECTION OF GOLDEN EAGLES IN SOUTHWESTERN IDAHO

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ABSTRACT.—We measured spatial use and habitat selection of radio-tagged Golden Eagles (*Aquila chrysaetos*) at eight to nine territories each year from 1992 to 1994 in the Snake River Birds of Prey National Conservation Area. Use of space did not vary between years or sexes, but did vary among seasons (home ranges and travel distances were larger during the nonbreeding than during the breeding season) and among individuals. Home ranges were large, ranging from 190 to 8,330 ha during the breeding season and from 1,370 to 170,000 ha outside of the breeding season, but activity was concentrated in small core areas of 30 to 1,535 ha and 485 to 6,380 ha during the breeding and nonbreeding seasons, respectively. Eagles selected shrub habitats and avoided disturbed areas, grasslands, and agriculture. This resulted in selection for habitat likely to contain their principal prey, black-tailed jackrabbits (*Lepus californicus*). Individuals with home ranges in extensive shrubland ($n = 3$) did not select for shrubs in the placement of their core areas or foraging points, but individuals in highly fragmented or dispersed shrublands ($n = 5$) concentrated their activities and foraged preferentially in jackrabbit habitats (i.e. areas with abundant and large shrub patches). As home ranges expanded outside of the breeding season, individuals selected jackrabbit habitats within their range. Shrubland fragmentation should be minimized so that remaining shrub patches are large enough to support jackrabbits. *Received 1 May 1996, accepted 6 May 1997.*

IN SOUTHWESTERN IDAHO, the demography and behavior of Golden Eagles (*Aquila chrysaetos*) are closely associated with variation in the abundance of black-tailed jackrabbits (*Lepus californicus*). Jackrabbit populations fluctuate, peaking at 7-to-12 year intervals (Johnson and Peek 1984). More eagles lay eggs and produce more offspring when jackrabbits are abundant than when jackrabbit populations crash (Steenhof et al. 1997), and eagles use alternative prey when jackrabbits decline (Steenhof and Kochert 1988). The importance of jackrabbits to eagles suggests that eagles should locate territories and concentrate foraging activities in habitats most likely to contain jackrabbits. We tested this hypothesis by relating spatial-use patterns of eagles to habitats associated with black-tailed jackrabbits. We then could indirectly describe habitat use by eagles relative to their main prey and quantify habitat characteristics meaningful to land managers.

Although descriptions of average behavior may be most easily understood by biologists and translated into management policy, they do not capture variation among individual animals. If such variation is substantial and ignored by focusing on population averages, conservation strategies and biological descriptions will be inaccurate and rarely effective. Describing individual variation, attempting to understand it, and using this to provide context-specific management recommendations would be preferable. Furthermore, many animals select and use resources at various scales (Allen and Starr 1982, O'Neill et al. 1988, Wiens 1989).

Here, we explore individual variation in Golden Eagle diet, spatial use, and habitat selection and show that, although certain habitat types are consistently preferred, the scale at which individuals exhibit selection for them is variable and dependent on landscape attributes and possibly individual experience. This is likely to be common in long-lived, permanent residents that maintain year-round, all-purpose territories, such as Golden Eagles (Beecham and Kochert 1975, Dunstan et al. 1978,

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TABLE 1. Golden Eagle territories where behavior, productivity, and home-range characteristics were studied, Snake River Birds of Prey National Conservation Area, 1991 to 1994.

Number of eagles		Individuals used in home-range estimation			Years locations were used in home-range estimation			
Captured	Instrumented	Sex	Age	Capture date	1991	1992	1993	1994
Black Butte								
2	1	M	Ad	12 Nov 91		X	X	X
Beercase								
2	2	M	Ad	18 Jan 92		X	X	X
Wildhorse								
2	2	F	Ad	14 Oct 91		X	X	X
		M	Ad	16 Dec 92			X	X
PP&L 119								
5	4	M	Ad	19 Feb 91	X	X	X	
		F	Ad	23 Oct 92		X	X	X
		M	Subad	11 Mar 94				X
Pole 369[a]								
0	0	F	Subad	17 Dec 91			X	
Grand View Sand Cliff								
2	2	F	Subad	17 Dec 91	X			
		M	Ad	24 Oct 92		X	X	X
Ogden								
1	1	M	Ad	14 Dec 92		X	X	X
Beecham								
1	1	M	Ad	22 Nov 91	X	X	X	X
Cabin								
12	2	F	Ad	06 Dec 91	X	X	X	X
		M	Ad	12 Apr 94				X

[a] Individual moved from Grand View Sand Cliff to Pole 369.

Collopy and Edwards 1989), because learning and experience may shape behavior (Mayr 1974).

METHODS

Site selection and trapping.—We studied Golden Eagles on 9 of 20 historically occupied territories (defended areas including nesting and foraging sites) along a 140-km stretch of the Snake River canyon (from Walter's Ferry to C. J. Strike Reservoir) within the Snake River Birds of Prey National Conservation Area (NCA). Approximately 75% of historically occupied territories were actually occupied during our study. We selected our subsample of territories to provide a representative sample of currently occupied landscapes in the NCA (none was inactive for more than 5 years from 1970 to 1991, four had >50% of the area within a 2.66-km radius circle centered at traditionally used nests burned by wildfires during the previous 10 years, and four had <30% of this area burned). One territory was added in 1993 when a radio-tagged female left her territory and joined an untagged eagle at a new site.

From 1991 to 1994, we captured 27 individuals in target territories (Table 1). Sex was determined by observations of copulation and measurements of body mass and footpad length (Edwards and Kochert 1986). Thirteen birds were instrumented with 65-g, solar-assisted transmitters secured by a 10-g harness of 19-mm wide Teflon webbing and a leather sternum patch; two were instrumented with 15-g tail-mounted transmitters. Transmitters may have reduced productivity in one year of study but did not influence behavior and spatial use (Marzluff et al. 1997). More than one individual was captured and radio-tagged in some territories because of transmitter failure or removal, eagle dispersal, and deliberate attempts to catch both breeders.

We monitored the behavior and productivity of radio-tagged Golden Eagles at eight territories during 1992, nine during 1993, and eight during 1994 (Table 1). Both the male and female were tagged in one of the eight territories in 1992, in two of the nine territories in 1993, and in three of the eight territories in 1994. To avoid concerns over pseudoreplication, we used the territory, not the individual on the territory within a year, as the experimental unit unless otherwise noted.

We captured eagles with radio-triggered bow nets (1991 and 1994), noosed lures (1991), and padded leghold traps (1991, 1992, 1993, 1994; Bloom 1987). We observed traps from 1 to 2 km away and broadcast noises from two-way radios buried near traps to reduce the frequency of catching nontarget species.

Location estimates and behavior.—Instrumented eagles were selected randomly and followed for 6-h observation periods, three to four days per month. Eagles in each territory were followed approximately weekly to balance observation effort across territories. We located eagles for visual observation, then continuously recorded time and activity data, particularly noting where hunting forays occurred and characterizing habitats in those areas. Locations were plotted (± 100 m) in the field on 1:24,000 scale topographic maps assisted by aerial photographs. Locations were obtained for all perched birds, all extreme points used by birds each day, and most points where birds soared. Perched locations included roost sites as well as hunting and resting sites. We also estimated the location of all copulations, undulating flights, and hunting attempts. Travel routes among perches or soaring areas were recorded, but estimates of point locations along these routes were not made. We used all observations on both members of the pair to determine the location of hunting attempts and prey captures. Hunting forays were any flights that included an attempt to capture prey (i.e. a steep dive or chase of potential prey).

Breeding status and habitat.—We considered eagles to have laid eggs if one member of the pair was seen in an incubating posture, or if eggs were seen. In 1992 and 1993, nestlings at sites tended by radio-tagged parents were banded and marked with uniquely numbered patagial tags to aid in observations within territories during the winter and to identify these birds within their parents' territories.

In a concurrent study, Knick et al. (1997) determined areal coverage of habitats from Landsat thematic mapper satellite imagery classified into big sagebrush (*Artemisia tridentata*)/green rabbitbrush (*Chrysothamnus viscidiflorus*), winterfat (*Ceratoides lanata*), salt-desert shrub (*Atriplex confertifolia, A. canescens, Sarcobatus vermiculatus*), grassland (*Poa secunda, Bromus tectorum, Sitanion hystrix*), cliff, and water. They also delineated all areas used for agriculture since 1979 (including fallow fields) from a composite of the 1979 Snake River Birds of Prey vegetation map (USDI 1979), 1993 Bureau of Reclamation agriculture maps, and the classified satellite imagery. Resolution of the habitat map was 50 m (resampled from 30-m pixels in the satellite image). Knick et al. (1997) used >5% ground cover of shrubs to separate shrub and grassland classes. Accuracy of the classification in separating shrub and grassland areas was 80%; accuracy in separating individual habitat classes was 64% (Knick et al. 1997).

Knick and Dyer (1997) developed an index of black-tailed jackrabbit habitats from a multivariate analysis that included number of agriculture cells, a habitat diversity index, number of shrub cells, shrub patch characteristics, and an index of landscape patchiness. The habitat index, scaled into 10% intervals, represented the probability of similarity of the habitat at each 50-m gridded cell in a Geographical Information System map to the mean habitat vector associated with jackrabbits. We used habitat associations of jackrabbits during low population phases and spring/early summer seasons. These were the conditions during the majority of our eagle observations, but jackrabbit population phases and season have little effect on jackrabbit habitat associations (Knick and Dyer 1997). We emphasize that the map of the jackrabbit habitat index did not predict the actual presence of jackrabbits, but rather the similarity of a given cell to habitats used by jackrabbits.

Analyses.—We used all unique locations visited by eagles during an observation session in home-range analyses rather than using a time interval to select "independent" locations. Use of unique locations reduced dependency by removing repeatedly visited locations within a sampling day, but it did not reduce the estimation of the maximum area used by an eagle. However, because many locations within a range were visited repeatedly each day and these tended to be near the center of the range, the exclusion of repeat locations resulted in an expansion of core areas. Because different radio-tagged individuals breeding within a given territory showed similar ranging habits, we used all unique locations from both eagles to define the home range associated with a territory. The nest site constituted a single observation for home-range analyses, even though it was visited multiple times.

We separated our locations into two seasons, breeding and nonbreeding. We defined breeding as the time from when eagles were first observed building nests or incubating until the end of the postfledging dependency period or the breeding attempt failed; nonbreeding included all times not within the breeding period. Therefore, seasons were of different duration for each individual territory.

We analyzed all four years of data using a two-factor repeated-measures ANOVA, with travel distances by year and season as the repeated measures. In this analysis we used only the five territories that were observed every year and where transmitter failure did not limit observations. Mean seasonal travel distances did not differ among years ($P = 0.95$); therefore, we pooled data across years and used data from eight territories to examine seasonal and territorial differences in travel distance using a two-factor (season and territory) ANOVA.

We used Ranges V software (Kenward and Hodder 1995) to calculate a variety of home-range estimates for comparative purposes, but we used only selected methods for analysis of habitat use and seasonal differences in home-range size. We used concave polygons with edge length restricted to half the minimum range diagonal to represent eagle home ranges. Concave polygons were most appropriate for estimation of habitat available to foraging eagles within their home ranges because they minimized territory overlap, included all known locations of eagles, and did not rely upon statistical distributions of locations. Harmonic-mean and convex-polygon methods were less satisfying because their reliance on the statistical distribution of locations resulted in extrapolation beyond locations we knew eagles visited, and, as a consequence, included extensive overlap between adjacent territories that we did not observe in the field.

We investigated habitat selection at three scales. First, we determined if eagles selected or avoided certain habitats in establishing a home range by comparing habitat used in concave polygon home ranges with habitat available within the study area. We defined available habitat as that area on either side of the Snake River canyon within the maximum travel distances observed for radio-tagged birds. Buffer areas, derived from maximum travel distances, were determined separately for the breeding and nonbreeding seasons. Second, we determined if eagles selected or avoided certain habitats within their home range by comparing the habitat used within core areas defined by hierarchical, incremental cluster analysis with a "nearest neighbor" joining rule (Kenward 1987) with habitat available within each individual's concave home range. We examined habitat in clusters that included 90 and 95% of locations separately. Most territories showed little change in the rate of area increase for cluster polygons that included from 20 to 90% of the locations but typically increased sharply thereafter, both in area within ranges and size variation between ranges, which indicated that the remaining 5 to 10% of locations were outliers. Third, we determined if foraging habitat was selected from within high-use areas by comparing the habitat within 100 m of locations where we saw eagles attempt to capture prey with the habitat available within core areas.

We determined the importance of habitat use with selection ratios (proportion of habitat class used/proportion of habitat type available) for each habitat type (Manly et al. 1993). We normalized selection ratios by using their natural logarithm. We viewed the individual territory as our sampling unit and calculated average selection ratios for our sample of territories. We calculated a 95% confidence interval around each ratio average after a Bonferroni adjustment for multiple comparisons. Selection ratios that did not include 0 in their confidence interval were evidence of significant ($\alpha = 0.05$) avoidance (ratio < 0) or selection (ratio > 0). We used compositional analysis (Aebischer et al. 1993) to test for individual differences in selection or avoidance of habitats.

RESULTS

SPATIAL-USE PATTERNS

Travel distance.—Distance traveled from the nest varied among individuals and between seasons. Eagles traveled farther from their nests outside of the breeding season ($\bar{x}$ = 3,036.1 ± SE of 241.6 m, n = 248) than during the breeding season ($\bar{x}$ = 1,046.8 ± 366.6 m, n = 121; repeated-measures ANOVA, F = 9.1, df = 1 and 4, P = 0.04). Annual variation in distance traveled was not significant (multivariate F = 0.05, df = 2 and 3, P = 0.95). However, individuals differed in travel distance between seasons (interaction of individual and season in two-way ANOVA without repeated measures, F = 2.29, df = 7 and 353, P = 0.03). Males ($\bar{x}$ = 1,963.7 ± 251.0 m, n = 253) and females ($\bar{x}$ = 2,094.2 ± 401.0 m, n = 116) traveled similar distances (F = 0.08, df = 1 and 365, P = 0.78).

An individual's travel distance from the nest was related to behavior (Fig. 1). Most of the extreme travel distances were hunting forays or undulating flights. A few individuals did most of their hunting (n = 2) and undulating (n = 2) near the nest.

Home range.—Similar patterns of travel also were reflected in individually and seasonally variable home ranges. Home-range estimators in Table 2 are for comparative purposes; we limited our discussion to concave polygons, which best described the total area used by eagles, and to clusters that removed extreme travels and defined high use (i.e. "core") areas.

Eagle breeding ranges encompassed 190 to 8,330 ha and expanded to 1,370 to 170,000 ha outside of the breeding season (Table 2). The average size of ranges was 2,280 ± SD of 2,625 ha (n = 8) during the breeding season and 30,484 ± 59,909 ha (n = 8) during the nonbreeding season. The large standard deviations resulted from extreme variation among individuals.

Home-range boundaries have remained fairly consistent for many years. Three of the territories we studied (a, b, i) also were studied

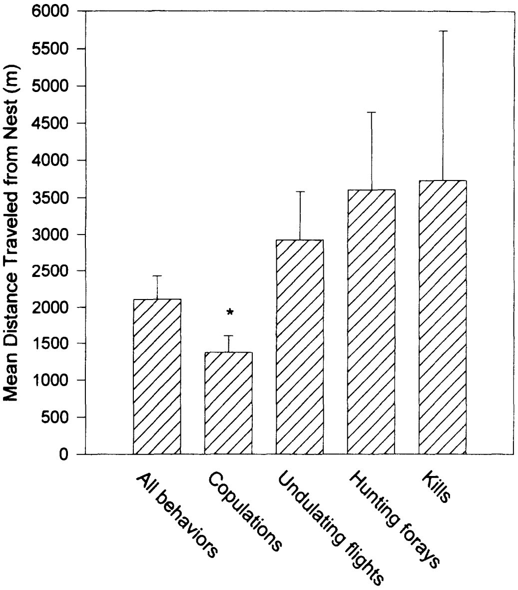

FIG. 1. Distances traveled by adult Golden Eagles where copulations, undulating flights, hunting forays, and kills were observed. Travel distance was calculated for each individual ($n = 9$) and averaged (± SE) across individuals. Significantly (*, $P < 0.05$) extreme average travel distances are indicated when the 95% confidence interval around the travel distance for a particular activity does not include the average travel distance to all locations.

with radiotelemetry in the 1970s (Dunstan et al. 1978). Home-range sizes in the 1970s and 1990s were similar (two ranges were larger and one was smaller in the 1970s than in the 1990s; $\bar{x}$ absolute difference in convex polygons = 1,256 ± SE of 413 ha), and ranges in the 1990s overlapped those from the 1970s by an average of 57.6 ± SE of 15.8%.

Breeding ranges of neighboring pairs overlapped only slightly ($\bar{x} = 3.7 \pm 1.7\%$, $n = 10$; Fig. 2A), suggesting territorial behavior. Interactions between neighbors were rarely observed because of the mutually exclusive territories. Expanded ranges outside of the breeding season overlapped neighboring ranges more than during the breeding season ($\bar{x} = 22.1 \pm 9.4\%$, $n = 10$; Fig. 2B) and included foraging areas frequented by wintering and nonbreeding eagles.

Nonresidents were captured in three territories (a, d, i) outside of the breeding season. Ten were captured in one territory (i), and only two offspring of residents were among those captured (one in territory d and one in i). Aggression between residents and nonresidents was extremely rare within and outside of the breeding season.

Eagles concentrated their activity within several frequently used cores. Cores defined by clusters of similar use indicated that 95% of the eagle locations were within 14.4 ± 3.1% of their breeding ranges and 25.3 ± 5.8% of their nonbreeding ranges (Fig. 2A, B). Ninety percent of the locations were within 6.9 ± 1.7% of breeding ranges and 12.6 ± 3.2% of nonbreeding ranges.

PREY

Black-tailed jackrabbits, Townsend's ground squirrels (*Spermophilus townsendii*), and Rock Doves (*Columba livia*) were the most commonly observed prey taken by eagles during our years of study (Fig. 3). Prey taken within and outside of the breeding season differed, with ground squirrels dominating the breeding season and jackrabbits dominating the nonbreeding season (comparing numbers of jackrabbits, ground squirrels, Rock Doves, and other prey for 1992 to 1994; Fisher's exact test, $P = 0.02$). Use of jackrabbits peaked in 1992 and then declined. Rock Doves, reptiles, yellow-bellied marmots (*Marmota flaviventris*), and Nuttall's cottontails (*Sylvilagus nutallii*) were taken more frequently as jackrabbit use declined.

Jackrabbits varied in importance among individual eagle pairs (pooled data from 1992 to 1994; Fisher's exact test, $P < 0.001$ for six pairs with $n \geq 6$ captures). One pair (b) took predominantly (8 of 10 captures) jackrabbits. However, the other pairs took jackrabbits much less frequently (jackrabbits comprised $\leq 7\%$ of the prey taken by pairs a, f, g, and h). Rock Doves, waterfowl, and marmots comprised the remainder of the prey taken.

HABITAT SELECTION

Vegetation.—Eagle territories occurred along a gradient of shrubsteppe habitats from big sagebrush, winterfat, and green rabbitbrush to salt-desert shrubs. Additionally, wildfires burned significant portions of some territories prior to our study, resulting in varying amounts of grassland among territories (Fig. 2A, B).

Selection of habitat classes.—The variation in

TABLE 2. Estimated areas (ha) of home ranges (concave and convex polygon, harmonic mean) and core areas (cluster analysis) of Golden Eagle territories (letters denote territories in Figures 2 and 5). Data combined across years and birds but analyzed separately for nonbreeding (N) and breeding (B) seasons.

Season	*n*	Concave 100%	Convex 100%	Harmonic 100%	Harmonic 95%	Core 95%	Core 90%
Black Butte (a)							
N	489	1,376	1,610	2,373	847	485	102
B	312	1,071	1,175	2,670	827	289	161
Beercase (b)							
N	298	11,261	18,541	61,792	10,110	2,581	938
B	325	8,331	9,759	22,929	5,536	1,535	565
Wildhorse (c)							
N	261	36,925	36,925	109,280	29,073	2,729	2,115
B	96	663	875	1,314	1,021	127	74
PP&L 119 (d)							
N	250	6,076	6,762	16,621	6,110	1,535	755
B	112	1,032	2,290	13,686	4,206	254	120
Pole 369 (e)							
N	22[a]	318	450	559	254	159	136
B	94	506	985	2,331	446	53	35
Grand View (f)							
N	297	176,010	207,069	614,675	86,810	6,387	2,035
B	116	194	336	877	94	30	5
Ogden (g)							
N	233	4,443	4,697	9,135	3,352	1,125	738
B	121	2,576	4,304	15,046	3,251	658	366
Beecham (h)							
N	453	3,721	4,625	16,582	2,001	487	194
B	277	3,055	3,471	29,818	323	86	31
Cabin (i)							
N	167	4,061	4,332	9,721	3,698	1,314	494
B	95	1,321	3,793	11,155	1,311	337	127

[a] Range sizes suspect owing to small sample size.

vegetation among territories was evident when we compared habitat classes found within breeding and nonbreeding ranges with available habitats within 4.5 km (the average maximum travel distance during the breeding season) or 9.5 km (the average maximum travel distance during the nonbreeding season) of the canyon rim. Most eagle home ranges had more sagebrush/rabbitbrush, more cliff/rock outcrop, less grassland, and less agriculture than expected from availability (see Table 3). Variation in selectivity among eagles was large (Table 3), and the resulting habitat composition of home ranges varied significantly among individuals (compositional analysis; breeding season, $\lambda = 0.16$, $\chi^2 = 16.5$, df = 5, $P < 0.01$; nonbreeding season, $\lambda = 0.20$, $\chi^2 = 14.4$, df = 5, $P < 0.05$). Most variation was due to varying amounts of sagebrush/rabbitbrush, salt-desert shrubs, grassland, and rock outcrop in home ranges. Individuals were more consistent in including less winterfat, agriculture, and water than expected based on availability in their ranges, especially during the breeding season (Table 3).

Eagle selection for shrubland and avoidance of grassland and agriculture was accentuated when we compared habitats in core areas with those available within each individual's home range (see Table 3). Avoidance of agriculture was significant and consistent among individuals during both seasons, especially within 90% core areas. Most individuals avoided grassland and selected shrubland, but individual variation precluded overall significance (Table 3).

Use and availability of habitats.—Selection coefficients are proportions and can mistakenly

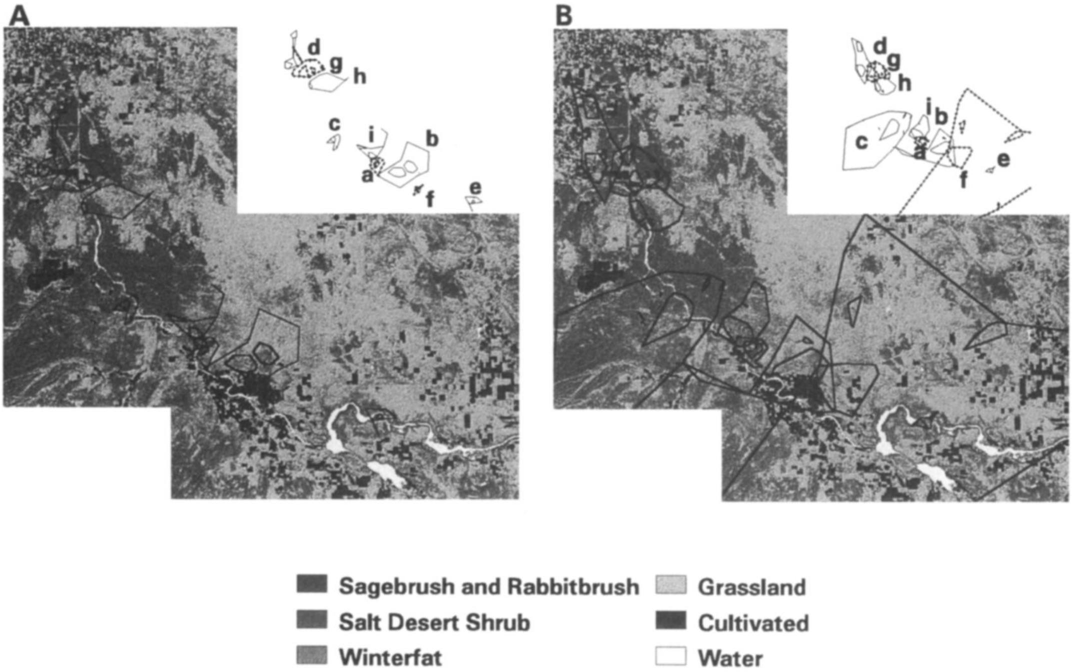

FIG. 2. Home range (solid lines, concave polygons) and core area (polygons within home ranges, 95% use area, cluster analysis) of eagles during (A) and outside of (B) the breeding season. Habitat of the study area is shown in the background to illustrate variation in shrub, grassland, and agriculture among territories. Small letters denote territory identification.

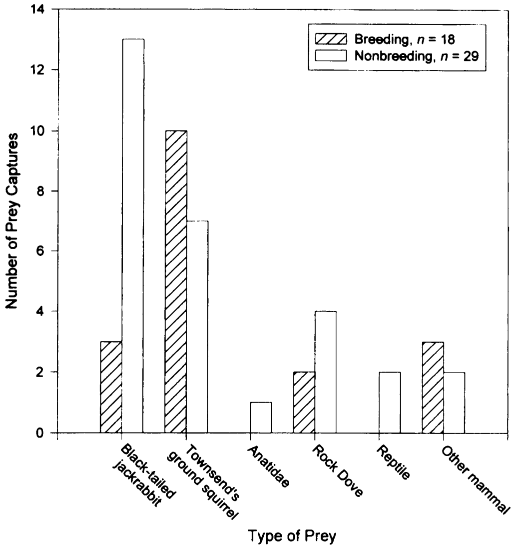

FIG. 3. Prey items captured by Golden Eagles, 1991 to 1994.

indicate strong selection or avoidance of very rare habitats because small absolute differences in use and availability are proportionately much larger than are similar absolute differences between common habitats. This potential problem contributed to the general avoidance of winterfat and water, and selection for cliff habitats (Table 3). The availability and use of these three habitats were very low (Fig. 4A, B, C).

Avoidance of agriculture was unlikely to be an artifact of habitat rarity (Fig. 4). Agriculture was avoided by all but one eagle, even though it represented as much as 24% of the available habitat. The individual that selected a core area with a relatively large amount of agriculture during the breeding season (Individual d) appeared to select agriculture because its territory had a substantial amount (18%) of agriculture available. Selection for agriculture in the nonbreeding season (Fig. 4A, B) and around foraging points (Fig. 4C) was suspect because the availability of agriculture used to compute those selection coefficients was very small.

TABLE 3. Average selectivity ($\bar{x} \pm$ SE) by nine Golden Eagles for habitat types at three scales. The mean selection coefficient (ln[habitat use/habitat availability]) indicates general avoidance (negative values) or preference (positive values) for each habitat class. The number of eagles selecting each class (use > availability) is shown to indicate consistency of habitat selection among individuals.

	Nonbreeding season		Breeding season	
Habitat class	Selection coefficient	No. eagles	Selection coefficient	No. eagles
Home range				
Sagebrush/rabbitbrush	−0.03 ± 0.23	6	0.12 ± 0.21	7
Salt-desert shrub	−0.49 ± 0.42	4	0.05 ± 0.53	3
Winterfat	−0.84 ± 0.55	4	−1.92 ± 0.82	2
Grassland/disturbed	−0.13 ± 0.09	3	−0.14 ± 0.13	3
Agriculture	−1.84 ± 0.96	3	−2.27 ± 0.94	3
Cliff	0.75 ± 0.48	5	0.29 ± 0.62	6
Water	−0.49 ± 0.42	3	−1.73 ± 0.85	2
95% Core area				
Sagebrush/rabbitbrush	0.13 ± 0.12	6	0.22 ± 0.16	7
Salt-desert shrub	0.24 ± 0.14	7	0.24 ± 0.32	5
Winterfat	−0.66 ± 0.31	2	−1.07 ± 0.51	2
Grassland/disturbed	−0.03 ± 0.09	5	−0.10 ± 0.09	2
Agriculture	−0.40 ± 0.21	1	−2.43 ± 0.80*	1
Cliff	0.55 ± 0.29	7	0.72 ± 0.21*	7
Water	−0.85 ± 0.80	6	−0.68 ± 0.91	3
90% Core area				
Sagebrush/rabbitbrush	0.26 ± 0.12	7	0.17 ± 0.22	7
Salt-desert shrub	0.20 ± 0.28	6	0.54 ± 0.40	5
Winterfat	−1.34 ± 0.51*	3	−1.69 ± 0.77	2
Grassland/disturbed	−0.13 ± 0.08	2	−0.20 ± 0.20	3
Agriculture	−3.16 ± 1.01*	0	−3.11 ± 0.85*	0
Cliff	0.86 ± 0.45	7	0.26 ± 0.70	7
Water	−1.72 ± 0.99	3	−1.93 ± 1.16	3

*, $P < 0.05$ (avoidance or preference different from availability).

Our evidence that sagebrush/rabbitbrush and salt-desert shrub habitats were selected was strengthened because these habitats were common yet included in home ranges, core areas, and around foraging points at frequencies that exceeded general availability. Sagebrush/rabbitbrush appeared to be more important than salt-desert shrub because it comprised a larger percentage of used habitats at all levels of comparison (Fig. 4).

Individual variability in selectivity for sagebrush/rabbitbrush tended to be correlated with the availability of those shrubs within a home range. Individuals tended to be more selective for sagebrush/rabbitbrush when it was relatively rare within their home range (depending upon season and level of comparison, r values ranged from -0.68 to -0.39, $n = 9$ in each case), but this relationship was only significant during the breeding season when selectivity within the 95% core area was compared with availability in the home range ($P = 0.04$, all other P-values < 0.29).

Avoidance of grassland by most individuals at all levels of comparison, especially during the breeding season, was not due to the rarity of grassland. Grassland was the most common habitat type regardless of season or level of comparison (Fig. 4). Even though it was used less than expected based on availability, grassland remained a dominant feature of eagle home ranges, core areas, and foraging locations, regardless of season. Individual variability in avoidance of grassland was not correlated with the abundance of grassland within home ranges. In most seasons and levels of comparison, eagles with the largest amount of grassland in their home range avoided it, but these relationships were weak (all r-values < 0.50, P-values > 0.17).

Selection for jackrabbit habitat.—Jackrabbit habitats varied significantly among territories (compositional analysis; breeding season, $\lambda = 1.29 \times 10^{-16}$, $\chi^2 = 329.3$, df $= 9$, $P < 0.001$; nonbreeding season, $\lambda = 2.57 \times 10^{-14}$, $\chi^2 = 281.6$, df $= 9$, $P < 0.001$). Five territories (a, b, f, h, i)

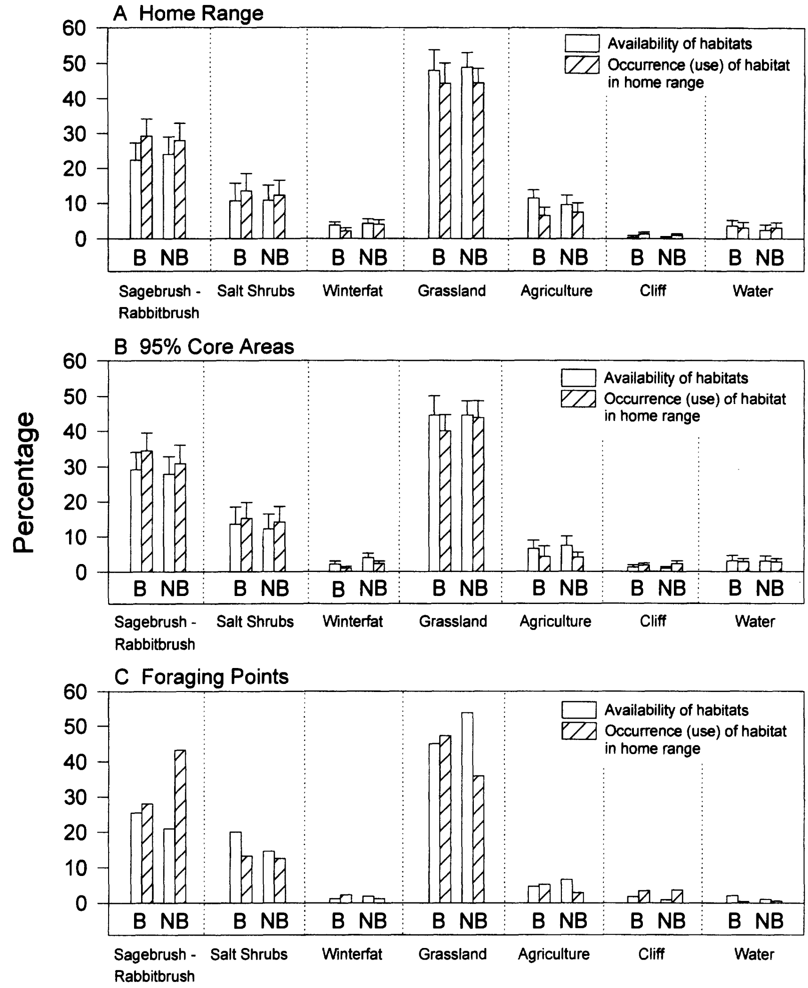

FIG. 4. Availability and use of habitat classes during the breeding and nonbreeding season. Use and availability is plotted for all nine territories in comparisons of home ranges with the study area (A) and of core area with home range (B). Data were insufficient to analyze habitat around foraging points separately for individuals, so all individuals were pooled (C). Values are $\bar{x}$ ± SE.

contained lower indexes of jackrabbit habitat, three territories (c, d, g) contained higher indexes, and one territory (e) contained intermediate indexes compared with availability in the study area (Fig. 5A, B).

Overall, eagles in the nine territories studied did not select or avoid habitats based on the probability of supporting jackrabbits (Table 4). However, some individuals were more selective than others. Five pairs (a, b, c, f, i) centered their 95% core areas within the best jackrabbit habitat available within their home range during the breeding season (Fig. 5A). All five pairs had territories containing less sagebrush/rabbitbrush than expected based on availability ($\bar{x}$ selection coefficient = −0.23 ± SE of 0.29) and less absolute occurrence of sagebrush/rabbitbrush ($\bar{x}$ = 20.8 ± 5.95%) than the other four pairs ($\bar{x}$ selection coefficient = 0.56 ± 0.12; Mann-Whitney U = 19, P = 0.03; $\bar{x}$ abundance = 39.6 ± 4.08%; U = 19, P = 0.03). Territories of pairs that selected for jackrabbit habitat had lower jackrabbit habitat indexes ($\bar{x}$ index = 0.34 ± 0.07) than territories of other eagles ($\bar{x}$ = 0.48 ± 0.06), but this difference was not significant (U = 14, P = 0.33).

In contrast to the breeding season, few eagles selected for jackrabbit habitats within core areas outside of the breeding season. Only one pair (i) had a 95% core area that included the best jack-

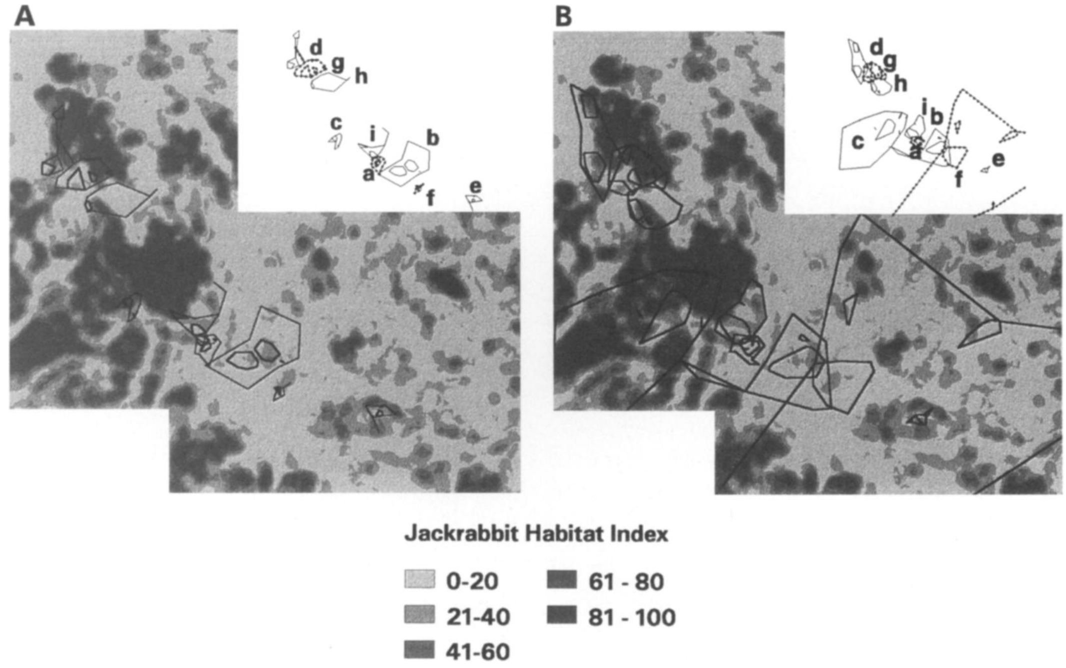

FIG. 5. Occurrence of black-tailed jackrabbit habitat in Golden Eagle home ranges (solid lines, concave polygons) and core areas (polygons within home ranges, 95% use area, cluster analysis) during (A) and outside of (B) the breeding season. Shading indicates the similarity of habitat at a given location to habitat used by jackrabbits. Progressively darker shading indicates habitats of progressively higher quality for jackrabbits. Small letters denote territory identification.

TABLE 4. Average selectivity ($\bar{x}$ ± SE) by nine Golden Eagles for black-tailed jackrabbit habitat types at three scales. The mean selection coefficient (ln[habitat use/habitat availability]) indicates general avoidance (negative values) or preference (positive values) for each habitat class. The number of eagles selecting each class (use > availability) is shown to indicate consistency of habitat selection among individuals.

	Nonbreeding season		Breeding season	
Jackrabbit index class	Selection coefficient	No. eagles	Selection coefficient	No. eagles
		Home range		
Highest 30%	−2.50 ± 1.15	3	−2.43 ± 1.23	3
Middle 40%	−0.03 ± 0.18	5	−0.64 ± 0.64	3
Lowest 30%	−0.16 ± 0.23	5	−0.23 ± 0.29	5
		95% Core area		
Highest 30%	−0.98 ± 0.65	1	−1.59 ± 1.00	2
Middle 40%	−0.02 ± 0.24	4	0.03 ± 0.28	5
Lowest 30%	0.01 ± 0.17	6	−0.61 ± 0.86	4
		90% Core area		
Highest 30%	−1.15 ± 0.64	1	−2.23 ± 1.23	2
Middle 40%	−0.58 ± 0.82	6	−2.00 ± 1.19	2
Lowest 30%	−0.01 ± 0.13	4	−0.48 ± 0.86	7

rabbit habitat available in its home range, and one other (b) had a 90% core that included some of its best jackrabbit habitat (Fig. 5B).

Foraging locations.—Selection of foraging locations within core areas differed between the breeding and nonbreeding season (Fig. 6). During the breeding season, individuals used winterfat shrublands, cliffs, and agriculture more frequently than expected; sagebrush/rabbitbrush was used in proportion to availability. As a result, eagles did not select foraging points in jackrabbit habitat within core areas during the breeding season. In contrast, during the nonbreeding season foraging points were primarily in sagebrush/rabbitbrush and along cliffs. Eagles also foraged within the best jackrabbit habitat inside their core areas during the nonbreeding season.

INTERRELATIONSHIPS OF HABITAT QUALITY, RANGE SIZE, AND EAGLE PRODUCTIVITY

Home-range size was not significantly related to eagle productivity. Breeding-range size tended to increase as the total number of young fledged from 1992 to 1994 increased ($r = 0.56$, $n = 9$, $P = 0.12$). Size of the nonbreeding range and size of core areas, regardless of season, were less closely correlated with productivity (all $Ps > 0.25$).

Two distinct groups of territories were evident during the breeding season. Pairs a, b, f, h, and i had a scarcity of shrubland associated with jackrabbits in their territories (Figs. 2, 5). In contrast, pairs c, d, and g had an abundance of shrubland associated with jackrabbits (Figs. 2, 5). Variation in habitat quality was not significantly related to differences in home-range size during the breeding season (high-quality territories, $\bar{x} = 1{,}423 \pm 586$ ha, $n = 3$; low-quality territories, $\bar{x} = 2{,}794 \pm 1{,}460$ ha, $n = 5$; $U = 5$, $P = 0.46$) or during the nonbreeding season (high-quality territories, $\bar{x} = 15{,}814 \pm 10{,}566$ ha, $n = 3$; low-quality territories, $\bar{x} = 39{,}286 \pm 34{,}221$ ha, $n = 5$; $U = 10$, $P = 0.46$). Territories in poor jackrabbit habitats had similar productivity compared with those in good jackrabbit habitats (total number of young fledged from 1992 to 1994; high-quality territories, $\bar{x} = 0.67 \pm 0.67$, $n = 3$; low-quality territories, $\bar{x} = 2.4 \pm 0.81$, $n = 5$; $U = 3$, $P = 0.17$).

DISCUSSION

Golden Eagles in our study varied considerably in patterns of spatial use. Size of the home range, size of the core area, and travel distances for various activities varied by two orders of magnitude among individuals. Habitat composition, potential prey abundance, and individual preferences developed by long-lived, permanent residents likely account for much of this variation. Eagles do not simply maximize home-range size, nor should they, because their breeding success was only weakly correlated with range size. Rather, eagles adjusted their ranging and foraging behavior to take advantage of the types and configuration of prey habitat found in the vicinity of their nest. Where high-quality jackrabbit habitat was abundant, pairs foraged evenly throughout the shrublands and had relatively small home ranges (e.g. pairs c, d, g; Figs. 2, 5). However, pairs in territories with little sagebrush/rabbitbrush (where jackrabbits were expected to be scarce) showed two patterns of space use that may reflect individual experiences: they either ranged over large areas and concentrated their use in the better habitats for jackrabbits (pairs b, f; Figs. 2, 5), or they restricted their activities to a small area of cliff and riparian habitat around their nests (pair a; Figs. 2, 5). Pairs that maintained small territories took fewer jackrabbits and more alternate prey, notably Rock Doves, waterfowl, and marmots found in the cliff and riparian habitats. Thus, quality of habitat is more important than quantity, but "quality" habitat comes under a variety of guises depending upon habitat availability and eagle prey selection (riparian habitat [Pair a], agricultural lands [Pair d], or shrublands [other pairs]).

Consistencies in habitat selection became more apparent as we refined our assessment of selection from the scale of the territory, to the scale of the core area, to the foraging point. This may indicate the scale at which eagles actually select habitats, or it may reflect the progressive reduction in use of excursive travels in our analysis. At progressively finer scales, where excursions are not included in the analysis, the majority of eagles selected shrubland and avoided grassland and agriculture. Sagebrush/rabbitbrush was the most important shrub type. Thus, habitat selection by resident

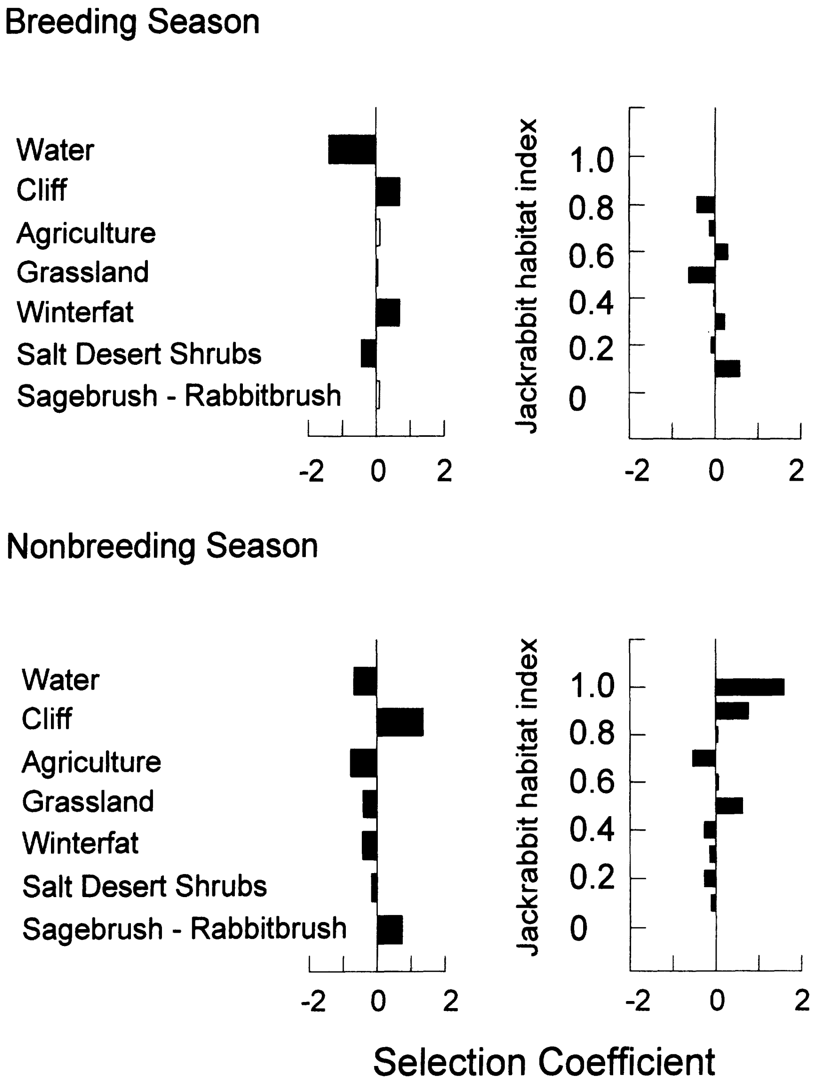

FIG. 6. Selection of foraging habitat within core areas by Golden Eagles. Selection coefficients (ln [percent habitat used / percent habitat available]) compare habitat within 100 m of foraging points with habitat available in 95% core areas during and outside of the breeding season. Selection is plotted separately for habitat classes and habitat quality for jackrabbits (0 is worst habitat, 1 is best habitat for jackrabbits). Vertical histograms show the relative preference (selection coefficient > 0) and avoidance (selection coefficient < 0) of each habitat or jackrabbit habitat-index category.

eagles was similar to selection previously documented for wintering vagrants (Craig et al. 1986).

Selection for sagebrush/rabbitbrush and the avoidance of agriculture and grassland resulted in most eagles foraging in habitats that had the potential to contain jackrabbits. Although our measure of habitat potential to support jackrabbits comes from the spring/summer season during a low population phase of jackrabbits, this is unlikely to influence our assessment of habitats because jackrabbits are found in the habitats rated as highest quality throughout the year, regardless of population cycling (Knick and Dyer 1997). However, the scale at which eagles selected jackrabbit habitats differed depending on the season and the characteristics of the home range. Outside of the breeding season, when even core areas were large, eagles selected foraging points in the best available jackrabbit habitat. During the breeding season, when ranges were smaller, entire core areas were in jackrabbit habitat, and foraging points within cores were in cliff, winterfat, and agriculture where other prey types (notably Townsend's ground squirrels and Rock Doves) occurred. Jackrabbit habitat was used frequently within breeding-season core areas, but use at the scale of foraging points was not selective because territories or core areas were already in the best jackrabbit habitat available. Eagles may be selective in good jackrabbit habitat, but our inability to partition habitat quality more finely precluded testing selection within the best jackrabbit habitat. The importance of selection at one scale to selection at other scales was further illustrated by the lack of selectivity for sagebrush/rabbitbrush within territories that already had a high percentage of sagebrush/rabbitbrush. Habitat selection needs to be investigated at several levels to understand fully how animals allocate their time among various habitats (Wiens et al. 1986, Aebischer et al. 1993).

Although the use of area varied widely among individuals in the nine territories, the use of area by eagles in a given territory varied little regardless of nest location, prey abundance, or identity of breeders. All of these factors varied among years, but home range size and range boundaries did not vary significantly among years. In fact, home-range boundaries changed little from the 1970s to the 1990s. Continued residency by at least one, and usually both, members of the pair, their individual use of perching and foraging habits, and the constraining effects of neighboring pairs on territory shape likely contributed to the stable patterns of spatial use within a territory. Long-term studies of marked individuals are necessary to accurately contrast variation in use of space between territories with variation within territories.

Despite annual stability in territory size and shape, physical defense of territories was rarely observed. Defense of boundaries against neighboring breeders was adequately accomplished by undulating flights (Harmata 1982, Collopy and Edwards 1989). Undulating flights were most often given at the edge of territories, rather than near nests (Fig. 1) and were least frequently given by pairs that had just formed (territory d, e; individuals were banded), suggesting that their function was territory maintenance rather than pair bonding. We routinely captured eagles that were not the tagged offspring of the present territory owners at food items we placed in territories during the nonbreeding season for trapping. Rather, these eagles were vagrant nonbreeders or winter residents. Lack of defense against nonterritorial eagles also was observed in Wyoming (Phillips and Beske 1982) and may be rare because eagles are not breeding and the risks of injury from fighting (Harmata 1982) outweigh any costs of losing foraging opportunities.

We documented the largest home-range sizes reported for this species. Many of the ranges in our study were within values previously reported for this study area and elsewhere (i.e. 500 to 9,000 ha; Dixon 1937, Tjernberg 1977, Dunstan et al. 1978, Phillips and Beske 1982, Collopy and Edwards 1989), but three individuals occupied much larger areas (individuals b, c, f; Fig. 2A, B). Increased size of home ranges often resulted from excursions, especially during the nonbreeding season. Core areas and 95% harmonic-mean ranges, which exclude excursions, are more similar in size to published home ranges. Excursions may have been accentuated during our study, which included a period (winter 1992–93 through 1994) when jackrabbit numbers were low and declining (Steenhof et al. 1997). However, excursions also may represent searches for breeding, as well as foraging, opportunities. They were not synchronized forays by the pair, and in one case the female from territory "f" included territory "e" in her travels; she settled and bred there the following spring. Like any estimate of home range, ours is dependent upon decisions made during data collection and selection of individual points for inclusion in analyses. However, our intensive, long-term observations that include several individuals occupying a given territory allowed us to make realistic estimates of actual space use by eagles.

MANAGEMENT IMPLICATIONS

Management of a healthy population of Golden Eagles in shrubsteppe habitats must focus on maintaining the native shrub community. Stands of sagebrush/rabbitbrush interspersed with grassland harbor sizeable populations of an important prey item, black-tailed jackrabbits (Knick and Dyer 1997). Our analysis demonstrates that eagles forage in areas without shrubs less than expected based on availability. Eagles were especially dependent upon shrub habitats when these shrub habitats were rare in the landscape.

Managers must recognize that although eagles range over large areas (>170,000 ha were used by one eagle), many concentrate their foraging in shrub habitats. Shrub (especially sagebrush / rabbitbrush) patch size appears to be an essential feature of all home ranges. Mean patch size for jackrabbit use of this habitat type was 5,000 ha, and the likelihood of observing jackrabbits increased with both increasing patch size and number of patches in the landscape (Knick and Dyer 1997). In managing the remaining large shrub areas in the landscape for eagles, we recommend that fragmentation by any disturbance not reduce the size of shrub patches below the mean patch size selected by jackrabbits. Patches slightly larger than this also should be maintained to accommodate maximum core areas during the nonbreeding season (6,387 ha; Table 2) and to provide habitat for vagrant and wintering eagles (observed in patches averaging 2,117 to 3,502 ha; Atkinson et al. unpubl. data). Individual variation in space use by eagles argues against using average values of home-range size in management recommendations. Rather, a variety of large and small areas could be suitable for eagles if they are managed to provide large shrub patches or rich alternative foraging areas (e.g. riparian zones).

ACKNOWLEDGMENTS

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THE INSTITUTE FOR
BIRD POPULATIONS

Breeding Burrowing Owl Survey for California

SPRING 2008 NEWSLETTER

FINAL SURVEY RESULTS ARE IN!

It required literally thousands of volunteer hours, but you did it! During the 2006 and 2007 breeding seasons, 396 volunteer surveyors contributed their time and effort to **The Institute for Bird Populations**' California Burrowing Owl survey, bringing the total number of 5km x 5km survey blocks visited to 860! We at IBP are very pleased with these results, and extend a heartfelt **THANK YOU** to everyone who participated.

The table at the right provides some summary results. As expected, the highest concentrations of Burrowing Owls occurred in the Imperial Valley and Southern Central Valley regions; perhaps more surprising was the relatively large number of owls in the Western Mojave region, particularly around Antelope Valley. More disappointing were the results from the Bay Area Interior region (112 pairs counted, down substantially from our count in the early 1990s) and the Modoc Plateau/Great Basin region, where we were unable to find *any* Burrowing Owls. Note that the numbers presented here are the actual numbers of owl pairs counted in each region, pooling results across both random and historical 'owl' blocks. We are now using statistical techniques to estimate regional population sizes based on these survey counts, and to compare the new regional and statewide estimates with results from our similar survey in the early 1990s.

Survey Region	**No. of Blocks Surveyed (2006-2007)**	**Pairs of Burrowing Owls Detected**
Bay Area Interior	89	112
Middle Central Valley	200	382
Northern Central Valley	48	10
Southern Central Valley	164	236
Central-western Interior	44	21
Southwestern Interior	68	150
Coachella Valley	20	49
Imperial Valley	15	521
Eastern Mojave	46	1
Western Mojave	67	94
Northern Mojave/ Eastern Sierra Nevada	38	1
Sonoran Desert	46	179
Modoc Plateau/ Great Basin	15	0
Total	**860**	**1,756**

Preliminary results suggest that Burrowing Owl distribution across the state may have contracted slightly since the early 1990s, particularly in the northern half of the state. Abundance appears to have declined slightly in many regions, though observed declines generally do not reach the threshold of statistical significance. Burrowing Owl numbers in a couple of metropolitan areas, particularly the San Francisco Bay Area and Bakersfield, have dropped substantially since the early 1990s. However, one bright spot is the Coachella Valley, where we detected no Burrowing Owls in the early 1990s, but where 49 pairs were observed during 2006-2007—many on the same individual census blocks that were found not to have owls in the 1990s.

Photo by Dave Herr

Recent, current and future activities…

Since the 2007 field season, IBP Biologist Bob Wilkerson has presented our preliminary results at two statewide meetings: a joint meeting of the California Burrowing Owl Consortium (CBOC) and California Partners in Flight in Davis, and another CBOC meeting in Brawley. More recently we have begun work on our Final Report to our funders (including the National Fish and Wildlife Foundation and the California Department of Fish and Game) as well as a manuscript for submission to a peer-reviewed scientific journal. We also intend to post detailed results on our website (www.birdpop.org).

Finally, many survey volunteers have asked about opportunities to participate in Burrowing Owl monitoring during 2008 and future years. We are grateful to everyone who has expressed interest. Although we think California's Burrowing Owls would be well-served by a long-term, volunteer-based monitoring program, we have not yet succeeded in securing funding to coordinate such an effort. Should funding become available in the future, we hope many of our 2006-2007 surveyors will heed the call to participate!

THANK YOU FOR YOUR TIME AND EFFORT!

The following individuals served as volunteer coordinators for their county or area in 2006, in 2007, or in both years: Marie Barrett, Rich Cimino, Chris Conard, Jeff Davis, Jimm Edgar, Mike Fisher, Dawn Garcia, Dan Guthrie, Darrell Hutchinson, Cheryl Johnson, Robin Leong, Krista Maney, Jessica Martini, Catherine Portman, Tom Ryan, Debra Shearwater, Ginny Short, Ian Taylor, Ruth Troetschler, Dave Wagner, and Carie Wingert.

The following individuals participated in censusing one or more survey blocks during either or both of the two survey years: Jennifer Albright, Chris Alderete, Diana Alleman, Lisa Allen, Russell Almaraz, Jerry W. Ambrose, Mary Ann Ambrose, Sundeep Amin, Chloe Anderson, Simon Avery, Joellyn Avery, Patricia Bacchetti, Jason Bachiero, Valerie Baldwin, Jack Barclay, Marie Barrett, Margaret Barson, Peggy Bartels, Candice Basham, Jeff Beauchamp, David Bell, Joyce Bender, Judy Bendix, Debbie Benham, Vern Benhart, Nicola Bennert, Josh Bennett, Murray Berner, Linda Bernhart, Milton Blatt, Diane Bodwin, Anita K. Booth, Brian Botham, Dawn Bradley, Steve Brady, Tricia Bratcher, Theresa Brennan, Craig Breon, Beverly Brock, Charles R.

Brown, Philip Brown, Debbi Brusco, Julie Bryson, Virginia Buchholz, Maureen Buffington Santo, Cheri Buskirk, Dotty Calabrese, Karlene Campo, David Carr, David W. Carr, Chuck Carroll, Randi Cassellius, Joyce Chang, Tony Chapelle, Sophie Chiang, David Chilton, Kirsten Christopherson, Jeff Church, Rich Cimino, Mareyn Clements, Richard Clements, Neil Clipperton, Wendy Cole, Barbara Coley, Roger Coley, James M. Collier, Judith A Collier, Chris Conard, David Cook, Mary Coolidge, Daniel S. Cooper, Curt Cotner, Erica Craven, Anne Crealock, Lori Cuesta, Cindy Curtis, Ken Curtis, Kirsten Dahl, Virginia L. Dallas-Dull, Ilma Dancourt, Larry Davidson, Jeff N. Davis, Karen DeMello, Susan Dieterich, Joan Dodson, Jim Dodson, Jed Douglas, Peter Drumer, Doug Drynan, Jim Dunn, Natasha Dvorak, R. Eckland, Jimm Edgar, Arthur L. Edwards, Linda Edwards, Lorna Elness, Mark Elness, Madi Elsea, Kevin Enus-Rempel, Laura Erickson, Janeann Erickson, Jake Estis, Mary Fajekers, Jonathan Feenstra, Stacey Feigekonwiesr, Hank Feilen, Jane Fielder, Megan Fisher, Mike Fisher, Tim Fitzer, Kasey Foley, Joel Forty, Bennie Fouch, Scott Frazer, Linda Freeman, Mary Freeman, Nick Freeman, Parker Fritch, Lillian Fuji, Harold Fukuma, Barry Furst, Dawn Garcia, Melisa Garcia, Maureen Geiger, Harriet Gerson, Brian Gibson, Neil Gilbert, Steven Glover, Dave Goodward, David Goodwawrd, Debbie Green, John F. Green, Richard Greene, Linda Greene, Christina Greutink, Dan Guthrie, Samantha Hafter, Portia Halbert, Catherine Halley, Devon Hammond, Lindsay Harman, Kristey Harrington, Carmen Hashagen, Ken Hashagen, Cole Hawkins, Priscilla Hawkins, Steve Hayashi, Ursula Heffernon, Lynn Hemink, J. Herman, Philip Higgins, Jon Hilbert, Carolyn Hinshaw, Allan Hollander, Lindsay Holt, Amber Holt, Kathryn Hood, Scott Huber, Liam Huber, Sherry Hudson, Bobby Huss, Darrell Hutchinson, Meighan Jackson, Sue James, Tim Jenkins, Phil Johnson, Vernon Johnson, Dave Johnston, Jennifer Jones, Douglas Joo, Linda Jordan, Corey Kaleshnik, Ginny Kaminski, Jerry Kaminski, Martin Karsch, M. Karsch, Lola Kashyap, Maral Kasparian, Guy Kay, David Keeling, Elena Keeling, Mary Keitelman, Lazan Keitelman, Ruth Kennedy, Stephen King, Judy Klink, Oliver Klink, Joanna Koob, Eva Kristofik, Nathan Krumm, Tim LaFlame, Kimya Lambert, Aleatha W. Landry, Steve Laymon, Cathie LaZier, Amanda LeClerc, Rod Lee, Sara Lee, Lora Leerskov, Robin Leong, John Lewis, Phyllis Lindley, Inna Litvin, Ivette Loredo, Kent D. Lou, Calvin D. Lou, Raymond Lukens, John Luther, Bill Lydecker, Greta Lydecker, Sarah Lydecker, Betty MacDonald, John MacDonald, Chris Macintosh, Jeanne Macneil, Shelly Magier, Ernie Maier, Colleen Martin, Cheryl McCloskey, Tim McClung, Kally McCormick, Walter J. McInnis, Gregory Meissner, Mary Beth Metcalf, Susanne Methvin, Jay Milee, Ashley Miller, Mel Miller, Karen Mitchell, Allison Mohoric, Richard Montijo, Alan Moore, Kris Moore, Richard

···Burrowing Owl Survey Hall of Fame···

Who found the greatest number of Burrowing Owls on a single block in 2007?

Bruce Wilcox, with 52 pairs on block # 3650-645 in the Imperial Valley

···Burrowing Owl Survey Hall of Fame···
Top Ten Block Surveyors for 2007

Name	Blocks Surveyed
Crispin Rendon	9
Bill Lydecker	7
Mike Fisher	6
John Luther and Susanne Methvin	6
Darrell Hutchinson	6
Chris Conard and Kimya Lambert	5
Dan Guthrie	5
Pam Williams	4
Ginny Short	4
Russell Almaraz	4

Moore, Nancy Mori, Suzanne Morron, Gerald Mugele, Jerre Murphy, Gordon Murphy, Sue Murphy, Ted Murphy, Jean Myers, George Nash, Kelley Nelson, Nancy Nelson, Wallace Neville, Renee New, Maggie Nunes, Michelle Ocken, D. O'Keefe, Rodney Olsen, Jennifer O'neal, Regena Orr, William Orr, Ed Pandolfino, Becky Parsons, Kay Partelow, Warren Patten, Jennifer Patten, Janna Pauser, Mark Paxton, Fraser Pembeiton, Barbara Pendergrass, David Perrin, Sarah Perrin, Marilynn Perry, Dawn Peterka, Paula Peterson, Randall Peterson, Susan Peterson, Carole Petrash, Shawn Petrash, David G. Philled, Sarah Pitzer, Ken Poerner, Kathy Porter, Marian Porter, Catherine Portman, Bob Power, Ted Raczek, Corina Rahmig, Troy Rahmig, Siddharthan Ramachandramurthi, Art Ramirez, George Rawley, Tricia Reed, Crispin Rendon, Virginia Rhodas, Michael Richard, Bob Richmond, Mike Richter, Matt Ritchie, Michael Robertson, Caroline Rodgers, Tobias Rohmer, Ann Romer, Sarah Ross, Patricia Rouzer, Jim Rowoth, Suzanne Ruckle, Tim Ruckle Jr., Tim Ruckle Sr., Ruth Rudesill, Michael Ruffino, Heather Ryan, Jeff Ryan, Thomas Ryan, Jennifer Rycenga, Donna Sadowy, Nancy Sage, John Santo, Fran Scarlett, Diana Scheel, Lexie Scheel, John Schick, Paul Schorr, Nancy Schorr, Mauricio Schrader, Steve Schwartz, Katie Schwartz, Steve Scott, Jeff Seav, Norman Self, Tracey Sharp, Kathy Sharum, Jackson Shedd, Kathy Shick, Robert Shields, Carolyn Short, Ginny Short, Rodney Siegel, Matthew Simes, Mike Skram, Dale M. Smith, Greg Smith, Michael W. Smith, Curtis Snyder, Tate Snyder, Susan Stanton, Jim Steinert, Sarah Stier, Steve Stocking, Mike Stockton, Brad Stovall, Bruce Strang, Nancy Strang, Linda Swanson, Dan Tankersley, Ian Taylor, Lynn R Thomas, Jennifer Thompson, Christine Tischen, Christine Tisher, Gene Troetschler, Ruth Troetschler, Jeff Trow, Lisa Twiford, Linda Vallee, Ann Verdi, Chuck Verturri, Chantal Villeneuve, Jamie Visinoni, Jim Waddell, Lisa Wadley, Dave Wagner, Annette Waite, Lucy Waite, Zach Wallace, Dee Warenycia, Dean Webb, Daniela Wersin, Kimberly West, Liz West, V. Wheeler, Jonathan Widdicombe, Bruce Wilcox, Bob Wilkerson, Anne Williams, Dan Williams, James Williams, M. Williams, Pam Williams, Bruce Williford, Michael Wilson, Carrie Wingert, Gary Woods, Aaron Works, Lois Wren, Rick Wulbern, Faith Yamane, Chad Young, Ryan Young, and Bill Zachman.

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CALIFORNIA Burrowing Owl Symposium

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Fire in the Southeastern Deserts Bioregion

Matthew L. Brooks and Richard A. Minnich

> ***Because of the inescapably close correlation between prevalence of fire and amount of fuel, deserts are characteristically less affected by fire than are most ecosystems … however, even though fire frequency and severity may be relatively low in any rating scale, their effect on the ecosystem may be extreme.***
> ***- Humphrey 1974, page 366.***

Description of Bioregion

Physical Geography

The southeastern deserts bioregion (desert bioregion) occupies the southeastern 27% of California (110,283 km^2 or 27,251,610 acres) (Miles and Goudy 1997). The desert bioregion is within the basin and range geomorphic province of western North America, and includes two ecoregional provinces comprised of five ecological sections. The American Semi-Desert and Desert Province (hot-desert province) includes the Mojave Desert, Sonoran Desert, and Colorado Desert sections in the southern 83% of the desert bioregion (Table 16.1). The Intermountain Semi-Desert Province (cold desert province) includes the Southeastern Great Basin and Mono sections in the northern 17% of the desert bioregion.

Table 16.1. General descriptions and lightning frequencies (1985-2001) in the ecological sections of the southeastern deserts bioregion.

Ecological section[a]	% of bioregion	Constituent ecological zones[b]	Predominant Küchler vegetation types[c]	Lightning strikes/ 100km^2/yr[d]
Mojave	61	low, mid, high, montane, riparian	desert shrub 58% barren 37%	30
Sonoran	12	low, riparian	barren 82% desert shrub 18%	25
Colorado	10	low, mid, riparian	desert shrub 57% barren 38%	12
SE Great Basin	10	high montane, riparian	desert shrub 74% juniper-pinyon 18%	29
Mono	7	high, montane, riparian	sagebrush 46% juniper-Pinyon 15%	32

[a] Miles and Goudy (1997)

[b] low elevation desert shrubland, middle elevation desert shrubland and grassland, high elevation desert shrubland and woodland, desert montane woodland and forest, desert riparian woodland and oasis (see detailed descriptions in the text)

[c] potential natural vegetation types (Küchler 1964) that constitute 15% or more of the ecological section.

[d] Bureau of Land Management lightning detection data (van Wagtendonk and Cayan, in press)

The geomorphology of the desert bioregion is characterized by isolated mountain ranges with steep slopes separated by broad basins containing alluvial fans, lava flows, dunes, and playas. Elevations range from -85 m (-280 ft) below sea level in Death Valley, to 4,328 m (14,200 ft) above sea level in the White Mountains. Soil taxa range widely from hyperthermic or thermic, aridic Aridisols and Entisols in the Colorado, Sonoran, and Mojave Desert sections, to thermic, mesic, frigid, or cryic, aridic, xeric, or aquic Alfisols, Aridisols, Entisols, Inceptisols, Mollisols, and Vertisols in the Mono and Southeastern Great Basin sections (Miles and Goudy 1997). This wide range in geomorphology and soil conditions translates into a wide range of vegetation and fuel types, which include arid shrublands and semi-arid shrublands, grasslands, woodlands, and forests.

Climatic Patterns

Although frontal cyclones of the jet stream pass through the region during winter (November through April), virtually the entire desert bioregion is arid due to rain shadows of the Sierra Nevada, Transverse, and Peninsular ranges (Chapter 2, this volume). Precipitation locally increases with orographic lift in desert ranges, particularly those that rise above 2,000 m (6,096 ft). From July to early September, the region experiences 10 to 25 days of afternoon thunderstorms from the North American monsoon originating in the Gulf of California and Mexico. Thunderstorm cells tend to concentrate over high terrain, especially the eastern escarpments of the Sierra Nevada, Transverse, and Peninsular ranges, in the mountains of the eastern Mojave Desert, and in the high basin and range terrain between the White Mountains and Death Valley. The average annual precipitation on valley floors ranges from 10 to 20 cm (3.9 to 7.9 in) in the Mojave Desert and southeastern Great Basin, to 7 to 10 cm (2.8 to 3.9 in) in the Colorado and Sonoran deserts. The average annual rainfall total at Death Valley (5.8 cm, 2.3 in) is the lowest in North America. Precipitation increases to 20 to 30 cm (7.9 to 11.8 in) in the mountains above 2,000 m (6,562 ft), 40 cm (15.8 in) in the White Mountains, and 60 cm (23.6 in) in the upper leeward catchments of the Sierra Nevada, Transverse, and Peninsular ranges. The percentage of annual precipitation falling during summer (May through October) ranges from approximately 20% in the southeastern Great Basin to 40% at the Colorado River in the Sonoran Desert.

Interannual variation in rainfall is relatively high compared to other California bioregions, resulting in highly variable frequency and extent of fires among years. High rainfall produces fine fuels that promote fire spread, especially in the hot desert sections where fuels are otherwise sparse. Low rainfall causes shrub mortality which reduces woody fuel moisture and may promote fire spread in the cold desert sections where woody fuel cover is relatively high, although low fine fuel loads caused by low rainfall is probably more limiting to fire spread. Multi-decadal variation in rainfall has also been significant, with periods of relatively high rainfall from the turn of the century until 1946, a mid-century drought from 1947 to 1976, and a period of high rainfall 1977 to 1998 (Hereford et al. in press). This approximately 30-year cycle, coupled with below-average rainfall from

1999 to 2004, suggest that another 30-year drought period may be establishing, which could lead to reduced frequency and size of fires in most of the desert bioregion entering the 21st Century.

The entire desert bioregion has a large annual range of temperature due to its isolation from the stabilizing influences of the Pacific Ocean. There is also large regional variability due to variable elevational relief. Average January temperatures on valley floors range from -3 to 0° C (27 to 32° F) in the northeastern Great Basin to 7 to 10° C (45 to 50° F) in the Mojave Desert, and 11 to 13° C (52 to 55° F) in the Sonoran and Colorado deserts. Temperatures decrease with altitude to about 0° C (32° F) at 2,000 m (6,562 ft) and -8° C (18° F) at 3,000 m (9,842 ft.). During summer, average temperatures vary near the dry adiabatic lapse rate due to intense atmospheric heating in the absence of evapotranspiration under high rates of insolation. July average temperatures on valley floors range from 18 to 20° C (64 to 68° F) in the northeastern Great Basin to 25 to 30° C (77 to 86° F) in the Mojave Desert and 30 to 35° C (86 to 95° F) in the Sonoran and Colorado deserts. Maximum temperatures average > 40° C (104° F) below 1,000 m (3,281 ft) elevation and occasionally reach 50° C (122° F) in Death Valley, the Colorado River, and the Salton Sea trough. In the desert mountains, average temperatures decrease to 20° C (68° F) at 2,000 m (6,562 ft) and 10° C (50° F) at 3,000 m (9,842 ft). The decrease in temperature with altitude results in rapid decrease in evapotranspiration which in phase with increasing precipitation results in corresponding increase in woody biomass of ecosystems. Light snowpacks 10 to 15 cm (3.9 to 5.9 in) deep can develop in winter but typically disappear by spring above 2,000 m (6,562 ft), although deeper snow of 100 cm (39.4 in) can persist into the spring in subalpine forests > 3,000 m (9,842 ft).

Relative humidity during the afternoon in the summer fire season, when fires are most likely to spread, is very low throughout the desert bioregion. Average relative humidity in July ranges from 20 to 30% in the northeastern Mojave Deserts to 10 to 20% in the Mojave, Sonoran, and Colorado deserts. Values are low because moisture of the Pacific Coast marine layer is mixed aloft with dry subsiding air masses upon dissipation of the marine inversion, as well as from high temperatures produced by convective heating of surface air layers. The lowest humidity of the year (frequently < 10%) typically occurs in late June, just before the arrival of the North American monsoon.

Lightning frequency is higher in the desert than in any other California bioregion (van Wagtendonk and Cayan in press). Lightning strikes/100km^2/year averaged 27 (sd = 16) from 1985 through 2000, ranging from 32 in the Mono to 12 in the Colorado Desert sections (Table 16.1). The bioregions with the next most frequent lightning strikes were the Northeast Plateau (22 strikes/100km^2/year) and Sierra Nevada (20 strikes/100km^2/year). Most lightning in the desert bioregion occurred from July through September (78%), resulting from summer monsoons which developed in the Colorado, Sonoran, and eastern Mojave deserts, and from summer storms that developed in the Sierra Nevada mountains and drifted into the southeastern Great Basin and Mono sections. Lightning also occurred primarily during daylight hours, with 81% between 0600 and 1800.

Ecological Zones

From a fire ecology perspective, much of the variation in the desert bioregion relates to patterns of fuel characteristics and fire regimes. Vegetation (fuels), topography, and lightning strikes per unit area vary locally with elevation, and elevational vegetation gradients are correlated positively with latitudinal gradients and ecotones with more mesic regions in the immediate rain shadow of the Sierra Nevada, Transverse, and Peninsular ranges. Accordingly, we consider elevation to be the primary determinant of fire ecology zones in the desert bioregion. The ecological zones described below are listed in order of increasing elevation, except for the riparian zone, which transcends many of the other zones.

Low elevation desert shrubland zone

This is the predominant ecological zone in the Sonoran Desert section. Major vegetation types include alkali sink vegetation and the lower elevations of creosote bush scrub (Munz and Keck 1959) and succulent scrub (Rowlands 1980). Surface fuel loads and continuity are typically low, hindering the spread of fire (Fig 16.1).

Fig.16. 1. The low elevation desert shrubland ecological zone. This photo shows a creosotebush scrub vegetation typical of the Sonoran Desert.

Middle elevation desert shrubland and grassland zone

This is the predominant ecological zone in the Mojave Desert, Colorado Desert, and Southeastern Great Basin sections, where it typically occurs as an elevational band above the low elevation zone and below the high elevation zone. It also occurs at the regional ecotone between the Mojave and Great Basin deserts. Major vegetation types include Joshua tree woodland, shadscale scrub, the upper elevations of creosote bush scrub (Munz and Keck 1959), blackbrush scrub, and desert scrub-steppe (Rowlands 1980). Surface fuel characteristics are variable, but loads and continuity can be relatively high compared to the low elevation zone, facilitating the spread of fire (Fig. 16.2).

Fig. 16.2. The middle elevation desert shrubland and grassland ecological zone. This photo shows a blackrush scrubland, which typically includes blackbrush, Mojave yucca, Joshua tree, and California juniper.

High elevation desert shrubland and woodland zone

This is the predominant ecological zone in the Mono section. It also occurs at the tops of most Mojave Desert mountains or just below desert montane forests, and along the margins of the Sierra Nevada, Transverse, and Peninsular mountain ranges where they intergrade with yellow pine forests. Major vegetation types include sagebrush scrub, pinyon-juniper woodland, and desert chaparral (Munz and Keck 1959). Surface fuel loads and continuity are high where sagebrush scrub and chaparral dominate, facilitating the spread of fire. However, surface fuels are replaced by very high loads of crown fuels in closed pinyon-juniper woodlands, where fires only occur under extreme fire weather conditions and are typically very intense (Fig. 16.3).

Fig. 16.3. The high elevation desert shrubland and woodland ecological zone. This photo shows a pinyon-juniper woodland.

Desert montane woodland and forest zone

This zone is very limited in total area, and occurs almost exclusively in the Mono and Southeast Great Basin sections. Major vegetation types include bristlecone pine forest and alpine fell-fields (Munz and Keck 1959). Surface fuels are typically sparse, separating patches of crown fuels and hindering the spread of fire (Fig. 16.4).

Fig 16.4. The desert montane woodland and forest ecological zone. This photo shows a bristlecone pine forest.

Desert riparian woodland and oasis zone.

This zone includes a diverse set of vegetation types that do not fit into any single elevational range. Vegetation types include oases and riparian woodlands, shrublands, grasslands, and marshes. Surface fuels loads and continuity can be very high, facilitating fire spread, although vertical continuity of ladder fuels and horizontal continuity of crown fuels are often insufficient to carry crown fires (Fig. 16.5).

Fig. 16.5. The desert riparian woodland and oasis ecological zone. This photo shows a riparian shrubland and woodland.

Overview of Historic Fire Occurrence

The primary factor controlling fire occurrence in the desert bioregion is fuel condition, specifically fuel continuity and fuel type. Where fuel continuity is low, as in most of the low elevation and desert montane ecological zones, fires will not typically spread beyond ignition points. Even where continuity is relatively high, fuelbeds may be comprised primarily of fuel types that do not readily burn except under the most extreme fire weather conditions. The coarse, woody fuels of pinyon-juniper woodlands in the high elevation ecological zone are a good example. Thus, variations in fuel condition are central to any attempts to evaluate past or current patterns of fire occurrence.

Prehistoric

Prehistoric fire regimes have not been quantitatively described for most of the desert regions of southwestern North America, largely because the usual tools for reconstructing fire histories, such as analyzing trees for fire scars or coring sediments in swamps or lakes for charcoal deposits, cannot be used where the requisite trees or lakes are not present. As a result, past fire regimes must be inferred indirectly from prehistoric vegetation studies or current observations and data.

Fossil packrat midden data suggest that most of the desert bioregion has been under arid to semi-arid conditions since the beginning of the Holocene (~10,000 years BP), with pinyon and juniper woodlands on upper slopes and at higher elevations, and low scrub and perennial grasslands in valleys and at lower elevations (Van Devender and Spaulding 1979, Koehler et al. 2005). Most interior basins in the desert bioregion did not support permanent lakes except those receiving runoff from the Sierra Nevada, Transverse, or Peninsular ranges. Thus, the major vegetation types that presently occur in the desert bioregion, and the ecological zones described in this chapter, were likely present in the desert bioregion throughout the Holocene, expanding and contracting relative to each other as they shifted up and down elevational gradients with periods of low and high rainfall.

The low elevation ecological zone probably contained low and discontinuous fuels, hindering fire spread and resulting in low intensity, patchy burns and long fire return intervals. Consecutive years of high rainfall would have increased fine fuel loads and continuity, and may have allowed fire to spread periodically in this ecological zone, especially were rainfall was highest along the western margins of the Mojave and Colorado deserts close to the Transverse and Peninsular mountain ranges.

The middle elevation, high elevation, and riparian zones likely had sufficient perennial plant cover to periodically carry fire in the prehistoric past without significant amounts of fine fuels. Because these fires would have been carried by relatively high cover of perennial shrubs and grasses, they were likely moderate intensity, stand replacing fires, as they typically are today.

Fuels in the desert montane zone were probably discontinuous resulting in small, patchy, and very infrequent surface or passive crown fires. Evidence of this is the presence of the long-lived (>3,000 years), but fire sensitive, bristlecone pine trees (*Pinus longaeva*).

It seems highly probable that fuel conditions and fire regimes have remained relatively constant across the desert bioregion during the Holocene, although their spatial distributions likely varied as the ecotones between vegetation formations shifted with alternating periods of low and high rainfall. Current climate conditions have generally persisted since ~1,440 years BP in the Mojave Desert (Koehler et al. 2005), supporting the supposition that relative distributions of fuel conditions and ecological zones have remained relatively constant during at least the latter part of the Holocene. It is also likely that fuel conditions and fire regimes have changed significantly since the late 1880s due to land use activities and invasions by non-native annual grasses. We discuss these changes in more detail below.

Historic

Livestock grazing can reduce perennial plant cover, especially cover of perennial grasses (Brooks et al. in press), which very likely has led to reduced landscape flammability since grazing began in the desert bioregion during the late 1880s. However, at the same time that fuels were reduced due to grazing, ignitions probably increased as fire came into use by livestock operators to convert shrublands into grasslands and increase forage production, especially in the Mono and middle to high elevations of the Southern Great Basin and Mojave sections. For example, rangelands in southern Nevada, southwestern Utah, and northwestern Arizona were extensively burned during the early 1900s to reduce shrub cover and promote the growth of perennial grasses (Brooks et al. 2003). Similar rangeland burns may have also been implemented in the southern and eastern Mojave Desert and the far western Colorado Desert, where summer rainfall occurs in sufficient amounts to support large stands of perennial grasses. However, most of the southern hot desert regions are too dry to support sufficient native fuels to carry fire, so even if ranchers tried to burn, they may have often been unsuccessful.

Analyses of historical aerial photos from 1942, 1953 to 54, 1968, 1971 to 74, 1998, and 1999 at Joshua Tree National Park indicate that there were periodic fires prior to 1942 (Minnich, 2003), during a 30-year period of relatively high rainfall that lasted until 1946 (Hereford et al. in press). However, most fires were <121 ha (300 acres) with the largest encompassing 607 ha (1,500 acres), and all occurred in the middle and high elevation ecological zones (Minnich, 2003). The spatial clustering of burns in some areas suggests that deliberate burning by humans was practiced, possibly to improve range production for livestock. During the mid-century drought, only three small fires occurred, all during the 1960s and in Joshua tree woodlands of the middle elevation ecological zone. Soon after the drought ended in 1977, fires again became more prevalent, but their size and numbers eclipsed what was observed prior to the mid-century drought. The first was a 2,428 ha (6,000 acre) fire in 1978, and the most recent was a 6,070 ha (15,000 acre) complex of fires that burned over a period of 5 days in 1999, both in the middle and high elevation ecological zones. These recent fires at Joshua Tree National Park were fueled largely by old stands of native trees, shrubs, and perennial grasses, but fire spread was additionally facilitated by stands of the non-native annual grasses red brome (*Bromus madritensis* ssp. *rubens*) and cheatgrass (*Bromus tectorum*), especially where fire passed through previously burned areas where cover of these grasses was especially high (National Park Service, DI-1202 fire reports).

Current

Records from land management agencies provide information on recent fires that can be used to reconstruct current fire regimes across the desert bioregion. We extracted data from fire occurrence records (DI-1202 reports) archived by the United States Department of the Interior and Department of Agriculture between 1980 and 2001 to create basic summaries for each of the five ecological sections in the California desert (Fig. 16.6, Table 16.2). This 21-year database is too short to capture the full range of potential burning conditions, because it was coincident with a period of above-average rainfall from 1977 to 1998 (Hereford et al. in press). However, it represents the best data available to approximate fire regimes since 1980 in the desert bioregion of California.

Table 16.2. Recent fire history (1980-2001)[a] in the ecological sections of the southeastern deserts bioregion.

Ecological section[b]	Total fires	Total Area burned	Fire frequency (fires/1000km^2/yr)	Annual area burned (ha/1000 km^2/yr)	Fire size (ha/fire)	Human: lightning fires	% of lightning strikes that resulted in fires[c]
Mojave	3158	69110	2.1	47	22	3.6	0.6
Sonoran	175	13217	0.6	47	76	7.5	0.2
Colorado	525	21340	2.2	88	41	44.2	1.8
Mono	1630	49292	9.6	292	30	0.5	2.0
SE Great Basin	90	5460	0.4	23	61	1.0	0.1
TOTAL	5578	158419	2.3	66	28	2.0	

[a] fire records (DI-1202 reports) of the Department of the Interior and Department of Agriculture, screened for errors as recommended by Brown et al. (2002).

[b] Miles and Goudy (1997)

[c] lightning frequency (van Wagtendonk and Cayan, in press) per lightning fires.

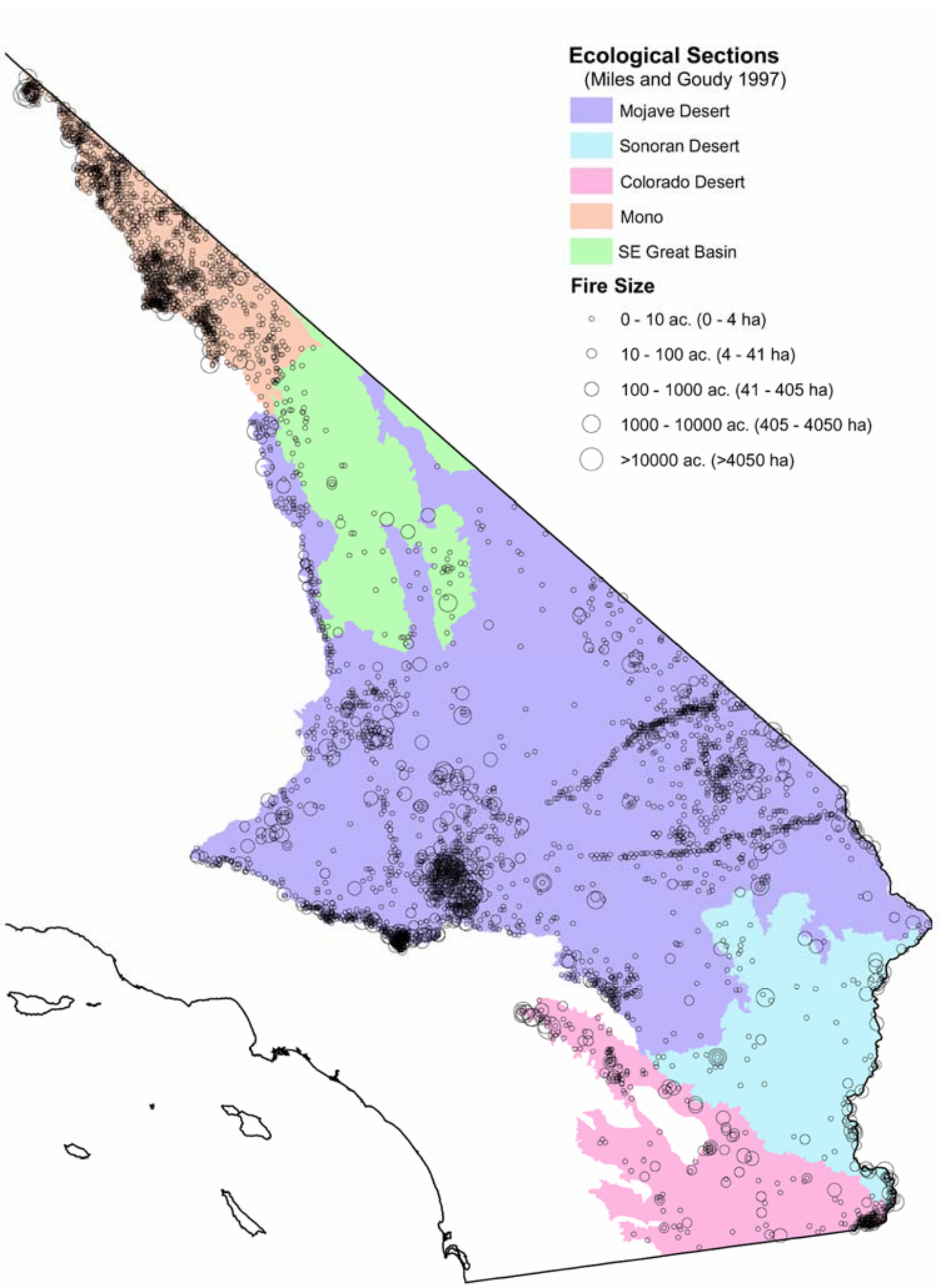

Fig. 16.6.Recent fire occurrences (1980-2001) in the five ecological sections of the Southeastern Deserts Bioregion.

The primary message from these fire records is that the proportion of total area that burned per year from 1980 to 2001 is very small, peaking in the Mono section at 0.3%/yr (292 ha/1,000 km^2/yr, Table 16.2), resulting in a fire cycle of 342 years in that ecological section. The annual fire frequency and area burned were highest in the Mono section, and lowest in the southern Great Basin section (Fig 16.6, Table 16.2), peaking from May through September. Among the hot desert regions, fire frequency was highest in the Mojave and Colorado deserts, and the annual area burned was highest in the Colorado Desert. The percentage of lightning strikes that resulted in fire was highest in the Mono and Colorado Desert sections, probably due to high fuel continuity caused by the prevalence of sagebrush steppe in the Mono section, and red brome dominated creosote bush scrub in the western Colorado section. The Colorado Desert section had the highest ratio of human:lightning caused fires. This is probably due to both the high human population density and agricultural activity in the Coachella and Imperial valleys, and the low frequency of lightning in the Colorado Desert (Table 16.1). The northern cold desert regions had the lowest frequency of fires caused by humans, probably due to its remoteness from major human population centers.

In a separate analysis of agency fire data from 1980 to 1995 in the Mojave, Colorado, and Sonoran desert sections, fires were found to be clustered in regional hotspots (Brooks and Esque 2002), where they were much more frequent and burned more proportional area than the desert-wide averages indicated in Table 16.2. Annual fire frequency increased significantly from 1980 through 1995 ($r^2 = 0.27$) (Brooks and Esque, 2002), but the increase was only significant in the low and middle elevation zones below 1,280 m (4,200 ft) ($r^2 = 0.32$, 1980 to 2001) (M. Brooks, unpublished data). A few areas burned three separate times during this 15-year interval. The increase in fire frequency was due to increased number of fires caused by humans, since the number of lightning-caused fires remained constant (Brooks and Esque, 2002). Another major contributor to increased fire frequency was a general increase in fine fuel loads caused by heightened dominance of non-native annual grasses beginning in the late 1970s (e.g. Hunter 1991) and continuing on through the 1990s (M. Brooks personal observation), probably the result of above-average rainfall from 1976 to 1998 (Hereford et al. in press). Although most fires were small and started along roadsides, most of the large fires occurred in remote areas far from major roads, and were typically started by lightning (Brooks and Esque, 2002).

Major Ecological Zones

In this section we describe the basic fire ecology of the predominant plant species in each ecological zone. We also discuss patterns of postfire succession, and interactions between plant communities, fire behavior, and fire regimes. More details on the fire ecology of a wider range of desert species can be found in other recent publications (Brown and Smith 2000, Esque and Schwalbe 2002).

Low Elevation Desert Shrubland Zone

This zone includes two primary vegetation types. Alkali sink vegetation occurs on poorly drained saline and/or alkaline playas, flats, and fans approximately -80 to 1,200 m (-63 to 3,937 ft) throughout all the ecological sections. Plant communities include iodine bush-alkali scrub, allscale-alkali scrub, Mojave saltbush-allscale scrub, and saltgrass meadow (Rowlands 1980). Creosote bush scrub vegetation occurs 0 to 1,200 m (0 to 3,937 ft) on well-drained flats, fans, and upland slopes of the Mojave, Colorado, and Sonoran Desert ecological sections. However, only the lower elevations below about 900 m (2,953 ft), were perennial plant cover is relatively low, are typical of the low elevation desert shrubland zone. Plant communities include creosote bush scrub, cheesebush scrub, succulent scrub (Rowlands 1980).

Fire responses of important species

Most shrubs in the low elevation zone do not survive after being completely consumed by fire (Humphrey 1974, Wright and Bailey 1982) (Table 16.3), but since many fires in this zone are patchy and of low intensity, plants frequently survive in unburned islands. Low fire temperatures in interspaces, and high temperatures beneath woody shrubs, likely results in relatively higher seedbank mortality for annual plants that frequent beneath-shrub than interspace microhabitats (Brooks 2002). A few perennial species that evolved to resprout after natural flooding disturbances often resprout after burning, such as desert willow (*Chiloposis linearis*), catclaw (*Acacia greggi*), smoke tree (*Dalea spinosa*), and cheesebush (*Hymenoclea salsola*) (Table 16.3). Cheesebush can have almost 100% survival rates even after being totally consumed by fire (Table 16.4). Cacti are usually only scorched during fires, as flames propagate through their spines but the stems do not ignite due to their high moisture content. Individuals with high levels of scorching typically die from uncontrolled desiccation that occurs postfire. Cactus regeneration can occur from resprouting of partially scorched plants, or rooting of fallen unburned stem fragments, but less frequently from establishment of new seedlings.

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Table 16.3. Fire responses of some dominant plant species in the southeastern deserts bioregion.

	Predominant Type of Fire Response[1]		
Lifeform	Sprouting	Individual	Species
Conifer	none	killed	bristlecone pine, limber pine, pinyon pine, Utah juniper
Hardwood	fire stimulated	top-killed	shrub live oak, salt cedar*, honey mesquite, willows
	fire stimulated	underburned	Fremont cottonwood,
Shrub	fire stimulated	top-killed	catclaw acacia, smoke tree, desert willow, fourwing saltbush, cheesebush, rubber rabbitbrush, spiny hopsage, antelope bitterbrush
	none	killed	Shadscale, blackbrush, creososte bush, brittlebrush, white bursage, snakeweed, cliffrose
Stem and Leaf Succulents	none	killed	Cacti
	fire stimulated	top-killed	Mojave yucca, bananna yucca, Joshua tree[2]
Herb	fire stimulated	top-killed	bulbs
	none	killed	annual forbs
Grass	fire stimulated	top-killed	perennial grasses (e.g. Galleta grass, Indian ricegrass, desert needlegrass, fountain grass*)
	none	killed	annual grasses (e.g. red brome*, Mediterranean grass*, cheatgrass*, six-week fescue).

[1] varies depending on fire intensity and percentage of plants consumed

[2] after initially resprouting, Joshua trees often die within 5 years if most or all of their foliage was scorched or consumed

* non-native species

Table 16.4. Survival rates of perennial shrubs after being unburned (0% of living biomass burned), scorched (1-10% of living biomass burned) or consumed (11-100% of living biomass burned) during 2.25ha (5.6acre) fires in August 1995 at three low elevation shrubland sites (M. Brooks, unpublished data).

species[a]	sample size	% survival[b]			notes on fire behavior[c]
		year 1	year 4	year 8	
Central Mojave Site					
white bursage					Fire did not spread from ignition points. Therefore, the litter beneath each shrub, but not the shrub itself, was ignited. Most creosote bushes were consumed, because accumulated dead branches beneath them provided supplemental surface fuels that increased flame residency time beneath them, and ladder fuels that helped carry fire up into the creosote bush canopies.
unburned	n=20	100	100	85	
consumed	n=20	20	20	10	
creosote bush					
unburned	n=25	100	100	100	
scorched	n=4	25	25	25	
consumed	n=21	0	0	0	
Southern Mojave Site					
creosote bush					Fire spread rapidly from a few ignition points and burned 50% of the site. Few shrubs were consumed due to low fuel loads beneath creosote bushes, and low cover of finely textured sub-shrubs.
unburned	n=25	100	100	100	
scorched	n=13	77	70	62	
consumed	n=12	8	8	8	
Western Mojave Site					
white bursage					Fire spread slowly from multiple ignition points, and burned 50% of the site. Most shrubs were consumed due to high fuel loads beneath creosote bushes and the presence of many finely textured sub-shrubs.
unburned	n=10	100	100	90	
consumed	n=10	20	20	20	
cheesebush					
unburned	n=10	100	100	60	
consumed	n=10	100	100	80	
creosote bush					
unburned	n=25	100	100	100	
scorched	n=8	88	75	75	
consumed	n=17	12	12	12	
Anderson wolfberry					
unburned	n=20	100	100	90	
scorched	n=5	100	100	80	
consumed	n=20	75	75	50	

[a] Dominant perennial plant species at each site. Not all were represented by both scorched and consumed plants. white bursage = *Ambrosia dumosa*, creosote bush = *Larrea tridentata*, cheesebush = *Hymenoclea salsola*, Anderson wolfberry = *Lycium andersonii*.

[b] Shrub survival was defined as possessing live leaf tissue, either on unburned or resprouted stems, when sampled during May of 1996, 1999, and 2003.

[c] Additional descriptions of the fires and study sites are reported in Brooks 1999.

The most frequently encountered and dominant shrub in this zone, creosote bush (*Larrea tridentata*), can have 25 to 80% survival rates 8 years postfire when it is only scorched (1 to 10% biomass loss), and 0 to 12% survival rates by year 8 when it is consumed by fire (11 to 100% biomass loss) (Table 16.4). Individuals with slight to moderate scorching displayed 30 to 40% survival in the Sonoran Desert in Arizona (Dalton 1962), and in general, fire intensity and duration is inversely correlated with sprout reproduction (White 1968).

The wide range in survival rates among creosote bushes appears to be associated with their variable physiognomy and variable fuel loads beneath their canopies and across the landscape, which translate into variable fire intensity and vertical continuity from surface to canopy fuels. Individuals with canopies in the shape of inverted cones tend to occur in water-limited environments (De Soyza et al. 1997), resulting in relatively low fuel loads beneath their canopies and across the landscape and a relatively low probability of being completely consumed by fire. In contrast, individuals with hemispherical canopies that extend to the ground tend to occur in less water-limited environments (De Soyza et al. 1997), resulting in higher fuel loads beneath their canopies and across the landscape and a higher probability of being completely consumed by fire. Resprouting in creosote bushes also probably varies throughout the extensive range of this species, especially at ecotones with vegetation types that support more frequent burning. For example, moderate (O'Leary and Minnich 1981, Brown 1984) to high (Brown 1984) rates of postfire resprouting were reported at the ecotone of the western Colorado Desert with shrubland vegetation in the Peninsular ranges.

Fire regime-plant community interactions

This is the zone that Humphrey (1974) was primarily referring to when he stated that in desert shrublands "…fires are a rarity, and the few fires that do occur cause little apparent damage to the various aspects of the ecosystem…" (pp. 337). This is largely because fuels are discontinuous and characterized by a sparse 8 to 15% cover of woody shrubs, and the large interspaces between shrubs are mostly devoid of vegetation, inhibiting fire spread (Fig. 16.1). A recent summary of fire regimes of the United States (Schmidt et al. 2002) assumed that Küchler's "barren vegetation type" (Küchler 1964), which covers most of the low elevation desert shrubland zone, is mostly devoid of vegetation and therefore fireproof. However, 9% of fires and 7% of the total area burned between 1980 and 2001 occurred within the barren vegetation type in the California desert bioregion. Thus, fires do occur in the low elevation desert shrubland zone, although not as frequently and over less area than in the other zones of the desert bioregion.

Fire behavior and fire regimes in this zone are affected primarily by the ephemeral production of fine fuels from annual plants. Years of high winter and spring rainfall can increase continuity of fine fuels by stimulating the growth of annual plants that fill interspaces and allow fire to spread (Brown and Minnich 1986, Schmid and Rogers 1988, Rogers and Vint 1987, Brooks 1999). Native annuals that produce some of the most persistent fuelbeds include the annual grasses six-weeks fescue (*Vulpia octoflora*) and small fesue (*Vulpia microstachys*), and the large forbs fiddleneck (*Amsinckia tessellata*), tansy mustard (*Descurania pinnata*), and lacy phacelia (*Phacelia tanacetifolia*), compared to a whole suite of smaller native forbs (119 species, Brooks 1999). Infrequently, successive years of high rainfall may have allowed these native annuals to build up fine fuel loads sufficient to carry fire across the interspaces between larger perennial plants. Low elevation fires carried by high loads of native annuals typically only burn dead annual plants and finely-textured sub-shrubs, leaving many of the larger woody shrubs such as creosote bush unburned. Thus, the historic fire regime was likely characterized by relatively small, patchy, low intensity surface fires, and a truncated long fire return interval (Table 16.5).

Table 16.5. Fire regime classification for desert shrubland zones.

Desert shrubland zone	*Vegetation Type*			
		Low elevation shrubland	Middle elevation shrubland and grassland	High elevation shrubland and woodland
	Temporal			
	Seasonality	Spring-summer-fall	Spring-summer- fall	Summer-early fall
	Fire Return Interval	Truncated long	Long	Long
	Spatial			
	Size	Small	Moderate to large	Moderate to Large
	Complexity	High	Multiple	Low to Moderate
	Magnitude			
	Intensity	Low	Moderate	Moderate to High
	Severity	Moderate	Moderate to high	High
	Fire Type	Surface	Passive crown to active crown	Active crown

The invasion of non-native annual grasses into the desert bioregion introduced new fuel conditions. Species such as red brome and Mediterranean grass (*Schismus arabicus* and *S. barbatus*) provide more persistent and less patchy fine fuelbeds than do native annual plants, breaking down more slowly and persisting longer into the summer and subsequent years (Brooks 1999). These new fuel conditions have the potential to increase the size, decrease the complexity, and shorten the time interval between desert fires, although fire intensity will likely decrease because fine herbaceous non-native fuels are replacing coarse woody native fuels. These fire regime changes have occurred over a small fraction of the low elevation ecological zone, and fire regimes over the vast majority of this zone still are within the historical range of variation.

Mediterranean grass is the most widespread and abundant non-native annual grass in the low elevation shrubland zone, although red brome may predominate under large shrubs or in the less arid parts of this ecological zone. Mediterranean grass has fueled fires as large as 41 ha (100acres) (Bureau of Land Management DI-1202 records), and interspace fuel loads of as little as 112kg/ha (100 lbs/acre) are sufficient to carry fire (Brooks 1999). Because these fires burn with low intensity, soil heating is negligible and most woody shrubs are left unburned.

The recent spread of Sahara mustard (*Brassica tournefortii*) throughout the low elevation shrublands has caused concern that this invasive mustard may introduce a significant new fuel type to the desert bioregion. During years of high rainfall this invasive annual can exceed 1 m (3.3 ft) in height with a rosette of basal leaves 1 m (3.3 ft) across, and even moderately sized plants can produce as many as 16,000 seeds (M. Brooks unpublished data). Plants can remain rooted and upright through the summer fire season, and when they finally do break off they blow like a tumbleweed and lodge in shrubs or fencerows, accumulating piles of fuels similar to Russian thistle (*Salsola* spp.). There are no records of fires specifically caused by Sahara mustard in the desert bioregion, however, the combination of this species with red brome in the understory helped fuel a 20.2 ha (50 acre) fire in creosote bush scrub in northwest Arizona (M. Brooks, personal observation). During the 5 years after this fire, Sahara mustard and red brome have come to dominate this site while the native creosote bush has yet to show signs of recovery.

Non-native annual plants that evolved in other desert regions will likely be most successful at persisting in the California desert bioregion. For example, Mediterranean grass and Sahara mustard respectively evolved in the arid Middle East and Northern Africa, and they have also successfully established in the desert bioregion (Brooks 2000, Minnich and Sanders 2000). At three sites in the western Colorado Desert, these non-native species successfully persisted through two major droughts, which occurred during the end of the 1980s and 1990s (R. Minnich, unpublished data). Their cover values in 1983, 1988, and 1990 through 2001 were comparable or higher than those of the non-native forb red-stemmed filaree (*Erodium cicutarium*), which is a poorer fuel source for fires (Brooks 1999), and compared to all native forbs combined.

Middle Elevation Desert Shrubland and Grassland Zone

This zone includes five primary vegetation types. The upper elevations of creosote bush scrub that generally occur at 900 to 1,200 m (2,953 to 3,937 ft) and contain higher perennial plant cover than the lower elevations of this vegetation type. Joshua tree woodland occurs on well-drained loamy, sandy, or fine gravelly soils of mesas and gentle slopes from 760 to 1,300m (2,493 to 4,265 ft) in the Mojave Desert and Southeastern Great Basin sections. Shadscale scrub occurs on heavy, rocky, often calcareous soils with underlying hardpan from 1,000 to 1,800m (3,281 to 5,906 ft) in the Mono, Southeastern Great Basin, and Mojave Desert sections. Blackbrush occurs on well drained, sandy to gravelly often calcareous soils from 1,000 to 2,000m (3,281 to 6,562 ft) in the southern Mono, Southeastern Great Basin and Mojave Desert sections. Desert scrub-steppe vegetation types are intermixed with a wide range of other plant communities from the low to the high elevation ecological zones, but they are most common in the middle elevation zone. Indian ricegrass scrub-steppe and desert needlegrass scrub-steppe typically occur were winter rainfall predominates within creosote bush scrub (Rowlands 1980). Big galleta scrub-steppe typically occurs in creosote bush scrub below 1,000 m (3,281 ft), and in Joshua tree woodland and blackbrush scrub above 1,000 m (3,281 ft).

Fire responses of important species

Higher fuel loads and more continuous fuelbeds in the middle elevation ecological zone result in higher intensity fires and higher frequency of top-killing in plants than in the low elevation zone. However, more species in this zone are likely to resprout after being top-killed. Perennial grasses such as desert needlegrass (*Achnatherum speciosa*), galleta grass (*Pleuraphis rigida* and *P. jamesii*), and Indian ricegrass (*Achnatherum hymenoides*) readily resprout after burning (Table 16.3). Spiny menodora (*Menodora spinescens*) and joint-fir (*Ephedra* spp.) often survive fire because their foliage does not readily burn. In contrast, some shrub species such as blackbrush (*Coloegyne ramosissima*) and winterfat (*Kraschennikovia lanata*) rarely survive burning.

Blackbrush is one of the more flammable native shrubs in the desert bioregion, due to its high proportion of fine fuels and optimal packing ratio. In the rare case that only a portion of a shrub is consumed, it may survive and resprout from the root crown. This resprouting was observed within the first few postfire years (Bates 1984), and these resprouts were still evident 20 years later (M. Brooks personal observation), at a site in the Mono section near Bishop, California. It is commonly thought that blackbrush stands take centuries to recover (Bowns 1973, Webb et al. 1988). However, analyses of historical photographs from Joshua Tree National Park and southern Nevada indicate that blackbrush stands can recover within 50 to 75 years (Minnich 2003, M. Brooks unpublished data), although other historical photographs from other locations do not indicate recovery within this time interval (M. Brooks, unpublished data). It seems probable that the ability of blackbrush to resprout after burning varies across its wide geographic range which extends from the Colorado Plateau and southern Great Basin on through the Mojave Desert.

Yucca species such as Joshua tree (*Yucca brevifolia*), Mojave yucca (*Yucca schidigera*), banana yucca (*Yucca baccata*), and Our Lord's candle (*Yucca whipplei*) are typically scorched as flames propagate through the shag of dead leaves that line their trunks. The relatively small size and more optimal packing ratio of dead Joshua tree leaves compared to dead Mojave or banana yucca leaves, increases the frequency at which they are completely burned. This may partly explain why Joshua trees are more frequently killed by fire. All four yucca species readily resprout after fire, but Joshua tree resprouts are often eaten by herbivores or otherwise die soon after burning. Postfire recruitment of new Joshua trees is infrequent, and likely occurs during years of high rainfall. No seedlings or saplings were observed in burns <10 years old, and only <10 individuals/hectare were present on burns >40 years old in Joshua Tree National Park (Minnich 2003). Joshua tree populations along the extreme western edge of the desert bioregion often resprout and survive more readily after fire than those further east (M. Brooks personal observation). A cycle of relatively frequent fire and resprouting can result in short, dense clusters of Joshua tree clones, such as those found near Walker Pass, in the western end of the Antelope Valley, and in pinyon-juniper woodlands at ecotones with the Transverse ranges. High resprouting rates of Joshua trees in these areas may have evolved in local ecotypes that became adapted to relatively high fire frequencies at the ecotone between the desert bioregion and more mesic ecosystems to the west.

Fire regime-plant community interactions

Some of the most continuous native upland fuels in the desert bioregion occur at the upper elevations of this zone, especially in areas dominated by blackbrush (Fig. 16.2). Invasive annual grasses have contributed to increased fire frequencies since the 1970's (Brooks and Esque, 2002), although the native perennial vegetation in this zone can at times be sufficient alone to carry fire during extreme fire weather conditions (Humphrey 1974). Between 1980 and 2001, 49% of all fires and 45% of total area burned occurred in Küchler's desert shrubland vegetation type, which is roughly analogous to the middle elevation ecological zone.

At the lower elevations within this zone, where creosotebush is co-dominant with a wide range of other shrubs and perennial grasses, fire spread is largely dependent on high production of fine fuels filling interspaces during years of high rainfall (Brown and Minnich 1986, Schmid and Rogers 1988, Rogers and Vint 1987, Brooks 1999). At higher elevations within this zone, where blackbrush is often the primary dominant plant, fire spread is not so dependent on the infilling of shrub interspaces during years of high rainfall and fire occurrence does not vary as much inter-annually compared to lower elevations (M. Brooks unpublished data). Thus, the historic fire regime was likely characterized by relatively moderate to large sized, patchy to complete, moderate intensity, surface to crown fires, and a long fire return interval (Table 16.5).

The post-fire response of plant communities in blackbrush scrub is illustrative of the general responses of other desert scrub communities in the middle and high elevation ecological zones. Blackbrush fires remove cover of woody shrubs which is soon replaced by equivalent cover of herbaceous perennials and annual plants (Brooks and Matchett 2003). Alien species such as red brome, cheatgrass, and red-stemmed filaree typically increase in cover after fire, but only if rainfall is sufficient to support their growth and reproduction. Recovery of blackbrush stands may occur within 50 years (Minnich 2003, M. Brooks, unpublished data), but perhaps more typically take over 100 years (Webb et. 1988, Bowns 1973).

Red brome is the dominant invasive grass at middle elevations in the California desert bioregion. This invasive grass produces higher fuel loads and fuel depths than does Mediterranean grass, and accordingly produces longer flame lengths that carry fire into the crowns of large woody shrubs more readily, producing more intense fires (Brooks 1999). Cover of red brome can become greater and more continuous after fire, promoting recurrent fire (Sidebar 16.1, this volume). This positive invasive plant/fire regime cycle (*sensu* Brooks et al. 2004) has shifted fire regimes outside of their historical range of variation in some regional hotspots (Brooks and Esque 2002), although fire regimes in most of the middle elevation zone are probably similar to historical conditions.

The recent invasion of the non-native annual grass African needlegrass (*Stipa capensis*) into the ecotone between the Colorado Desert and the Peninsular ranges in the 1990s has helped fuel at least one 243 ha (600 acre) fire (R. Minnich, personal observation). There are early indications that this species can survive relatively dry years, suggesting that it may spread and become another source of fine fuels that may further alter fire regimes in the desert bioregion.

High Elevation Desert Shrubland and Woodland Zone

This zone includes three primary vegetation types. Sagebrush scrub occurs in 1,100 to 2,800 m (3,600 to 9,186), although it can extend to 3,800 m (12,467 ft) in the White Mountains. Pinyon-juniper woodland occurs 1,300 to 2,400 m (4,265 to 7,874 ft), and can reach 2,700 m (8,858 ft) in the White Mountains. Both vegetation types occur in the Mono, Southeastern Great Basin, and Mojave sections. Among the pinyon-juniper vegetation types, the Utah juniper – single-leaf pinyon association is the most widespread, occurring in the Mono, Southeastern Great Basin, and eastern Mojave Desert ecological sections of California (Minnich and Everett 2001). The California juniper – single-leaf pinyon association occurs along the desert slopes of the Transverse ranges at the edge of the Mojave Desert section, with California juniper dominating below 1,700 m and single-leaf pinyon dominating above. Desert chaparral is the least prevalent of the major vegetation types in this ecological zone. It occurs on the middle slopes of the Transverse ranges adjacent to the Mojave Desert, and the Peninsular ranges adjacent to the Colorado Desert, below the mixed conifer forests, and in the same general elevation range as sagebrush scrub and pinyon-juniper woodland.

Fire responses of important species

Relatively high fuel loads result in high fire intensity, but plant mortality rates can vary widely among species. Wyoming big sagebrush (*Artemisia tridentate* ssp. *wyominensis*) is typically killed by fire, but it often re-establishes readily from wind-dispersed seeds. Cliffrose (*Purshia mexicana*) is typically killed by fire, whereas its close relative, antelope bitterbrush (*Purshia tridentata*), exhibits highly variable responses to fire, sometimes resprouting (Table 16.3). Interior chaparral species, such as *Quercus cornelius-mulleri, Q. turbinella, Cercocarpus betuloides, Arctostaphylos glauca,* and *A. glandulosa, Nolina* spp., either resprout or reseed soon after fire, but lower rainfall and sparser vegetation cover results in less frequent fire and slower recovery rates than is typical of cis-montane chaparral.

Pinyon pine (*Pinus monophylla*, *P. edulis*) and juniper (*Juniperus osteosperma*, *J. californica*) are typically killed by fire, but these woodlands can re-establish after 100+ years of fire exclusion. Juniper typically re-establishes from seed sooner than pinyon pine. Initial establishment of single-leaf pinyon pine appears to be delayed 20 to 30 years by sun scald and/or freeze/thaw soil heaving until the establishment of the shrub layer and young juniper trees which act as nurse plants (Wangler and Minnich 1996). The first pinyon recruits establish within the canopies of nurse plants, often near root axes. The establishment of a pinyon pine canopy after about 75 years eventually reduces freeze-thaw processes, setting off a chain-reaction of spatially random recruitment throughout old burns. Pinyons develop complete canopy closure after 100 to 150 yr which is accompanied by a decline in the surface vegetation, due apparently to shrub senescence and shade stress.

Fire regime-plant community interactions

Fuel continuity is similar to that of the middle elevation zone, but the fuels are generally more woody and difficult to ignite. In addition to high plant cover, the prevalence of steep slopes in this ecological zone facilitates the spread of fire. Due to the high biomass of woody fuels created by juniper and pinyon pine, and to a lesser extent sagebrush (*Artemisia* spp.), bitterbrush, cliffrose, and scrub oak (*Quercus turbinella*), the fires that do start are among the most intense encountered in the desert bioregion. Between 1980 and 2001, 33% of fires and 45% of the total area burned occurred in Küchler's sagebrush, juniper-pinyon, and chaparral vegetation types which are characteristic of the high elevation ecological zone.

Fire spread can occur most any year in sagebrush steppe, although it is more likely when fine fuel loads (especially cheatgrass and red brome) are high following years of high rainfall, or during periods of high winds and low relative humidity. Fires are patchy to complete, moderate intensity passive crown to crown fires, depending the continuity of the woody shrub fuels. Fire spread in pinyon-juniper woodlands is most probable when live fuel moisture and relative humidity are low and winds are high. When fires did historically occur, they were mostly large, intense crown fires, burning through woodland crown fuels. At the interface between sagebrush steppe and pinyon-juniper woodland, a surface to passive crown fire regime is the norm, as fire spreads through woody and herbaceous surface fuels and occasionally torches woodland fuels, especially younger trees. The historic fire regime was likely characterized by relatively large, patchy to complete, moderate intensity surface to crown fires, and a long fire return interval (Table 16.5).

Sagebrush stands generally require 30 to 100 years to recover following fire (Whisenant 1990). Where cheatgrass has dramatically shortened fire return-intervals, especially in the lower elevation Wyoming big sagebrush communities, sagebrush steppe has been converted to non-native annual grassland (Sidebar 16.1, this volume). In the higher elevation mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities, this type conversion is much less common, since the native shrubs and perennial grasses recover much more rapidly after fire.

Fire suppression coupled with removal of fine fuels by livestock grazing has allowed pinyon-juniper woodlands to encroach on sagebrush steppe across much of the western United States (Miller and Tausch 2001), including the Mono section of the desert bioregion. However, it is less likely that woodland encroachment has occurred in the more arid hot desert regions, due to low primary productivity rates. Recent resampling of 1929 to 1934 California Vegetation Type Map (VTM) survey plots reveal no significant changes in woodland densities at the western edge of the hot desert regions (Wangler and Minnich

1996). Pinyon-juniper woodlands adjacent to the Transverse ranges have experienced long periods between stand-replacement fires both before and after fire suppression began (fire rotation periods, ~450 years; Wangler and Minnich 1996).

Fires in pinyon-juniper woodlands are least frequent in open stands at lower elevations and more frequent in dense forests at higher elevations, in response to changing productivity and fuel accumulation gradients with increasing elevation and rainfall. The upper elevation ecotones between pinyon-juniper woodlands and mixed conifer forest are typically very narrow, due to truncated disturbance gradients related to fire behavior and stem mortality (Minnich 1988). The thin bark of pinyon pine prevents their survival in the frequent surface fire regime typical of mixed conifer forests. Alternatively, postfire surface fuels appear to lack sufficient biomass to support short-period burns, and as canopy closure occurs in pinyon and juniper woodlands, surface fuel loads and continuity are further reduced. Thus, a historical discontinuity in fire return intervals probably existed along the ecotones between mixed conifer forests and pinyon woodlands in which understory surface fires at high elevations shift to long-period stand-replacement crown fires at lower elevations in response to differences in stand structure, fire behavior, and tree survivorship (Minnich 1988).

Desert Montane Woodland and Forest Zone

There are two primary vegetation types in this ecological zone. Bristlecone-limber pine forests occur on well-drained, shallow, dolomitic soils from 2,600 to 3,800 m (8,530 to 12,467 ft) in the Inyo, White, Panamint, Funeral, and Grapevine mountains. Alpine fell-fields occur above timberline, primarily in the White Mountains. Small white fir forest enclaves also occur on north-facing slopes from 1,900 to 2,400m (6,234 to 7,874 ft) in the New York, Clark, and Kingston mountains of the Mojave Desert section (Rowlands 1980).

Fire responses of important species

The flagship tree species of this ecological zone, bristlecone pine and limber pine (*Pinus flexilis*), have thin bark which makes them susceptible to mortality during fires (Table 16.3). Although most individuals are struck by lightning by the time they are 1,000 years old, strikes may not result in the entire tree burning, since many old individuals have scars resulting from multiple lighting strikes. The presence of ancient bristlecone pine individuals is testimony to the historical infrequency of fire. As a result, most plant species in this zone are not adapted to recovery from fire, although species associated with other periodic natural disturbances such as from colluvial erosion may be able to resprout after burning.

Fire regime-plant community interactions

Fuels are very discontinuous, but in contrast to the low elevation zone, ephemeral production by annuals during years of high rainfall adds very little to the fuel bed, due to shallow soils, low temperatures, and a short growing season. As a result, surface fires are extremely rare, and most fires that do occur spread through the crowns of pines only during extreme fire weather conditions, but even these fires are very small <1ha (2.5 acres). Between 1980 and 2001, <1% of all fires and total area burned occurred in Küchler's great basin pine, alpine meadows-barren, and mixed conifer vegetation types characteristic of the desert montane ecological zone.

Low productivity results in very low fuel loads and continuity in the desert montane forests. Except on steep, north-facing canyons, heavy fuels are widely spaced and fine fuels are low and relatively unflammable, making it difficult to carry fire in this landscape. Thus, the historic fire regime is characterized by truncated small, patchy, variable intensity, passive crown fires, and a truncated long fire return interval (Table 16.6).

Table 16.6. Fire regime classification for the desert montane woodland, and riparian woodland/oasis zones.

Desert montane woodland, and riparian woodland/oasis zone	*Vegetation Type*		
		Desert montane woodland	Riparian woodland/oasis zone
	Temporal		
	Seasonality	Summer-early fall	Spring-summer-fall
	Fire Return Interval	Truncated long	Short to moderate
	Spatial		
	Size	Truncated small	Small to moderate
	Complexity	Moderate	Low
	Magnitude		
	Intensity	Multiple	High
	Severity	Multiple	Multiple
	Fire Type	Passive Crown	Passive to active crown

Desert Riparian Woodland and Oasis Zone

Riparian woodlands occur primarily along the Colorado and Mojave river corridors adjacent to low elevation shrublands in the southern desert region. Other examples can be found in the Amargosa Gorge, Whitewater River, Andreas Canyon, and Palm Canyon. In the northern desert region, riparian woodlands occur along the Owens and Walker rivers and the many creeks along the east slope of the Sierra Nevada Mountains. Oasis woodlands occur in isolated stands such as the Palm Canyon, Thousand Palms, and Twentynine-palms oases in the Colorado Desert section.

Fire responses of important species

Woodland dominants such as Fremont cottonwood (*Populus fremontii*) honey mesquite (*Prosopis glandulosa*), and willows (*Salix* spp.) typically resprout after being topkilled (Table 16.3). However, resprouting individuals and seedlings are susceptible to mortality during recurrent fires. Oasis species such as Washington fan palm (*Washingtonia filifera*) benefit from frequent, low-intensity fire, which reduces competition for water from other plants growing at the surface, and allow new seedlings to become established.

Fire regime-plant community interactions

Fuel characteristics and fire behavior are extremely variable, due to the wide range of vegetation types that characterize the riparian zone. In general fuels are typically continuous and fuel loads high, but fuel moisture content is also often high. Fires may not carry except under extreme fire weather conditions. Thus, the historic fire regime is characterized by small to moderate sized, complete, high intensity passive to active crown fires, and a short to moderate fire return interval (Table 16.6).

In riparian woodlands the invasives saltcedar (*Tamarix* spp), and less frequently giant reed (*Arundo donax*), create ladder fuels that allow fire to spread from surface fuels of willow (*Salix* spp.), saltbush (*Atriplex* spp.), sedge (*Carex* spp.), reed (*Juncus* spp.), and arrow weed (*Pluchea sericea*) into the crowns of overstory Fremont cottonwood trees, top-killing them. After an initial fire, these invasive quickly recover and surpass their pre-fire dominance, promoting increasingly more frequent and intense fires which, can eventually displace most native plants (Sidebar 16.2, this volume).

In palm oases, Washington fan palms depend on surface fire to clear understory species and facilitate recruitment. However, these sites can be pre-empted by saltcedar as it rapidly recovers after fire. The ladder fuels saltcedar creates can also carry fire into the crown of Washington fan palms, increasing the incidence of crown fires (Sidebar 16.2, this volume)

Management Issues

Fuels Management

The deserts of southwestern North America are one of the fastest growing regions in terms of human populations in the United States. As human populations increase, so to do the number of people living at the wildland-urban interface, which complicates fire management in many ways (Chapter 19, this volume). Increasing human populations can also potentially change fuel characteristics, through increased air pollution which can increase deposition rates of atmospheric nitrogen, and potentially increase fine fuel loads (Brooks 2003). Burgeoning human populations can also increase the introduction rates of new plant species that could add new fuel components and fire hazards to the region (Chapter 22, this volume). Since fire spread is mostly limited by the availability of contiguous fuels, fuel management can be a very important tool for fire managers in the California desert bioregion, even though the areas in which it is used may be a small percentage of the total region.

Herbaceous fuel management

The fuel component of greatest concern in the desert bioregion is the continuous cover the non-native annual grasses red brome, cheatgrass, and Mediterranean grass that appear during years of high rainfall. Although populations of these non-native annual plants and their resultant fine fuel loadings wax and wane with annual and multi-decadal fluctuations in rainfall (Sidebar 16.1, this volume), they have changed fire behavior and fire regimes in many parts of the desert bioregion, especially in the low elevation ecological zone where their presence is almost a prerequisite for large fires.

Despite all the concern surrounding the non-native species already dominating the desert bioregion, new grass invaders such as fountain grass (*Pennisetum setaceum*), buffelgrass (*Cenchrus ciliare*), and African needlegrass, and invasive mustards such as Sahara mustard, may pose additional fire hazards in the future. For example, in the Sonoran Desert, buffelgrass invasion coupled with frequent fire has converted desertscrub to non-native grassland in Mexico (Búrquez et al. 2002), created fuels sufficient to carry fire in Arizona, and recently appeared in southeastern California (M. Brooks personal observation). Land managers who once lamented the damage caused by fires fueled by red brome in southern Arizona are even more concerned now about the potential effects of buffelgrass (S. Rutman, Organ Pipe Cactus National Monument, personal communication). Buffelgrass is currently being considered for addition to the Arizona Department of Agriculture, Noxious Weed List, due primarily to its ability to alter fire regimes (E. Northam, personal communication). Thus, fine fuels management should be closely tied to invasive plant management, because the predominant plant invaders in the southern part of the desert bioregion are relatively flammable herbaceous species (Brooks and Esque, 2002). This is important both from the perspective of managing invasive plant fuels that are currently present, and preventing the establishment of new invasive plants that may change fuel structure and potentially cause even greater fire management problems in the future.

Livestock grazing has been mentioned as a possible tool for managing fine fuels in the desert bioregion (Brooks et al. 2003, Minnich 2003). It may temporarily reduce fine fuel loads, and be effective for managing fuels in specific areas such as within the wildland urban interface. However, grazing may also reduce cover of late seral native plants and replace them with non-native annual and other early seral plant species (Brooks et. al 2003) that can be more flammable. Grazing treatments must be applied with attention to the potential responses of all dominant plant species, both in the short term based on the phenologic stage during which they are grazed, and in the long term based on their life history characteristics and inter-relationships among species.

Woody fuel management

Where native plant cover is sufficient to carry fire without the addition of fine fuels from non-native plants, coarse woody fuels are the major concern of fire managers. In the central and southern parts of the desert bioregion, blackbrush intermixed with perennial grasses, Joshua trees, and juniper produce the right mix of high fuel continuity, fuel loads, and fuel packing ratio that can cause large intense fires with frequent spotting ahead of the flaming front. Although infrequent, intense, stand-replacing fires are a natural part of blackbrush shrubland ecology, these types of fires are not desirable when they occur near human habitations, or where they may damage cultural resources such as historical buildings or pre-historical sites. Once these fires start, they often require indirect firefighting tactics to suppress, which complicates efforts to protect specific areas from burning. As a result, land managers and scientists are testing ways to reduce the chances of extreme fire behavior in this vegetation type where it occurs between Joshua Tree National Park and the communities of Yucca Valley and Joshua Tree (M. Brooks et al., unpublished data). They are comparing the effects of fire and mechanical blackbrush thinning on subsequent fuel conditions, fire behavior, and plant community structure. The goal is to find tools that will allow managers to manipulate fuel characteristics to reduce fire hazards near areas identified for protection from fire, while having minimal negative ecological effects, such as increased dominance of invasive non-native plants.

Sagebrush and pinyon-juniper fuels are the primary focus of fuel management in the northern parts of the desert bioregion, especially in the Mono section. Sagebrush intermixed with perennial grasses is generally considered to be a greater fire hazard than the blackbrush communities described above. A century or more of fire exclusion, livestock grazing, and climate change can also result in encroachment by pinyon-juniper woodlands into sagebrush steppe (Miller and Tausch 2001). This has been documented in the northeast bioregion of California (Schaefer et al. 2003), and has also occurred where rainfall is relatively high in the desert bioregion at the ecotone of the Great Basin desert with the Sierra Nevada Mountains (Anne Halford, botanist, BLM-Bishop Field Office). Dense stands of mature trees in that area increase the chance of intense, stand-replacing, crown fire. Unfortunately, these same mature woodlands are desirable for use as homesites, especially in the Mono section, complicating the implementation of fuels management treatments and the protection of homes during fires. Millions of hectares are planned for fuels reduction in the western United States (http://www.fireplan.gov), and much will involve thinning of smaller size classes of pinyon and juniper trees to allow surface fuels to increase, and moderate intensity surface fires to return to the ecotone between pinyon-juniper woodlands and sagebrush steppe. Because very little is known about the effectiveness of these treatments in changing fire behavior or the potential ecological effects of these treatments, a research project was recently begun to quantify the effects of pinyon and juniper thinning on subsequent fuel condition, fire behavior, and ecosystem variables at a site in northwestern Arizona (M. Brooks et al., unpublished data).

Where sagebrush and pinyon-juniper vegetation interface in the southern desert sections, they are either at high elevations far from major roads and human habitations, or they contain surface fuels of insufficient amount and continuity to carry fire. These stands only burn under extreme fire weather conditions. Analyses of aerial photographs and VTM survey data from the 1930s show no evidence of pinyon-juniper expansion in the southern parts of the California desert region (R. Minnich, unpublished data). Accordingly, management of pinyon-juniper fuels is not advisable in this region, except were needed for specific cultural resource or safety reasons.

Fire Suppression

There is specific concern about the effect of fire suppression activities on the federally threatened desert tortoise where it occurs in low and middle elevation zones (Sidebar 16.3, this volume). More generally, fire suppression in desert wilderness areas became a significant issue after the California Desert Protection Act (1994) applied this designation to many new areas. Wilderness areas often encompass mountain ranges in the desert bioregion, where locally high fuel loads from both native and non-native plants, and steep slopes, facilitate the spread of fire. Fire suppression options are generally more limited in these areas by the constraints outlined in wilderness management plans, and often the primary tactic is to wait for fire to spread down slope and attempt to stop it along pre-existing roads. This can result in large portions of desert mountain ranges burning during a single event. The question is, which causes greater ecological damage, activities associated with aggressive fire fighting (e.g. construction of hand or bulldozer control lines, fire retardant drops) or large-scale, sometimes recurrent, fire occurring where fires were historically small and infrequent? We recommend that suppression be a high priority where fire frequency has been recently high in regional hotspots and non-native grass fire cycles have become locally established (Brooks and Esque 2002), where local populations of non-native plants may be poised to expand their range and landscape dominance following fire (mostly in the middle elevation ecological zone), or where there are other management reasons to exclude fire. Otherwise, a let burn policy for natural fires may be appropriate.

Postfire Restoration

Burn Area Emergency Rehabilitation (BAER) teams have developed postfire restoration/rehabilitation plans after the large fires that have recently occurred in the Mono section (e.g. Cannon and Slinkard fires), and further south in the desert bioregion at its ecotone with the Transverse and Peninsular ranges (e.g. the Juniper Complex and Willow fires). Much of this effort is focused on protecting watersheds from soil erosion, and one of the common tools is the seeding of rapidly growing plants (Sidebar 20.1, this volume). In general, seeding treatments establish more readily in the cold deserts than in the hot deserts, although relative establishment rates and the ecological effects of seeding in these two regions have not been experimentally compared.

Postfire seeding may also be used to compete with and reduce the cover of invasive grasses associated with the grass-fire cycle (Sidebar 16.1, this volume). The idea is to replace highly flammable species such as cheatgrass with less flammable seeded species. Non-native perennial grasses such as crested wheatgrass (*Agropyron desertorum*) have been used to compete with and reduce cover of cheatgrass in Great Basin sagebrush steppe. However, there has been a recent move toward using native species in postfire seeding, which may not have the same effect as non-native perennial grasses in suppressing the growth of non-native annual grasses such as cheatgrass. A current study is evaluating the relative effectiveness of non-native versus native perennial grasses to compete with and reduce cover of cheatgrass after fires in sagebrush steppe in the Mono section, and at sites in the Great Basin and Colorado Plateau (M. Brooks, unpublished data).

Fire Management Planning

One of the biggest challenges in fire management planning is determining desired future conditions to use as management goals. In cases where historical fire regimes can be reconstructed (e.g. ponderosa pine forest), the natural range and variation of historical fire regime characteristics may be a realistic and appropriate target. However, management goals may be elusive where historical fire regimes cannot be easily reconstructed, such as in the desert bioregion where one must rely on indirect inferences.

Fire histories alone may not be enough to establish management goals when protection of specific natural or cultural resources are the primary management goal, or where plant invasions have changed the rules of the game. For example, if plant invasions have shifted fuel characteristics outside of their natural range of historical variation, then restoration of historical fire regimes may be impossible without first dealing with the invasive plants that are at the root of the problem (Brooks et al. 2004). Although it appears that fire regimes, and at least woody fuel conditions, across much of the desert bioregion may be within their historical range of variation, it is difficult to quantify the impact that non-native plant invasions have had, aside from recognizing that fire regimes have been altered dramatically in some regional hotspots (Brooks and Esque 2002). Further complicating this process are the effects of potential future changes in rainfall patterns (Hereford et al. in press), and levels of atmospheric CO^2 (Mayeaux et al. 1994) and nitrogen deposition (Brooks 2003), on fuel conditions and fire regimes. All of these potential variables need to be considered when determining fire management goals in the desert bioregion.

The recent mandate by federal land management agencies to create fire management plans for all management units has resulted in a flurry of activity as new plans are drafted and old plans are revised. In many cases, plans developed for desert management units are supported by relatively few scientific studies, due to the paucity of fire research that has been conducted in the desert regions of North America. Decisions on when and where fuels should be managed, fires should be suppressed or allowed to burn, or post-fire restoration projects should be implemented, are difficult to make given the limited data available. Recent reviews have attempted to provide land managers and others with current information on desert fire ecology and management (Brooks and Pyke 2001, Brooks and Esque 2002, Esque and Schwalbe 2002, Esque et al 2002, Brooks et al. 2003). Along these same lines, a primary purpose of this desert bioregion chapter is to provide additional information that can be used in the development of fire management plans in the deserts of southwestern North America.

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SIDEBAR 16.1. Ecological Effects of Non-native Annual Grasses

by Matthew Brooks and Richard Minnich

Non-native annual grasses in the genera *Bromus*, *Avena*, and others have become dominant components of many grasslands, shrublands, woodlands, and forests in western North America during the 20th century. These invasions have negatively affected native plant species by directly competing with them for limiting soil nutrients and water, and by altering ecosystem properties such as fuel characteristics and fire regimes. The positive feedback between non-native grass dominance and increased fire frequency, or the "grass/fire cycle" (D'Antonio and Vitousek 1992), is the most clearly understood and well-documented example of the more general "invasive plant/fire regime cycle" (Brooks et al. 2004).

Fire frequencies that have increased beyond their historical range and variation can have dramatic and far-reaching ecological effects. For example, invasion of the non-native cheatgrass (*Bromus tectorum*) has altered fuelbed characteristics and shortened fire return intervals from 30 to 100 years to 5 years in areas of the Great Basin (Whisenant 1990). This new fire regime promotes the dominance of cheatgrass over native species, resulting in large-scale conversions of high diversity, native sagebrush steppe to low diversity, non-native annual grassland. This vegetation change has negatively affected animals that require sagebrush steppe for forage and cover such as the sage grouse (*Centrocercus urophasianus*) (Sidebar 11.2, this volume), and prey species such as black-tailed jackrabbits (*Lepus californicus*) and the Paiute ground squirrel (*Spermophilus mollis*) which are important for golden eagles (*Aquila chrysaetos*) and prairie falcons (*Falco mexicanus*) (Knick and Rotenbery 1995, Knick et al 2003). Although similar large-scale higher-order effects have not been documented in the Mojave, Colorado, or Sonoran deserts, non-native grass/fire cycles have degraded habitat for the desert tortoise (*Gopherus agassizii*) in localized hotspots within these desert regions (Brooks and Esque 2002, Sidebar 16.3 this volume).

Invasive plant/fire regime cycles represent ecosystem shifts to alternative stable states which will likely persist unless fuels, climate, or ignition patterns significantly change (Brooks et al. 2004). For example, non-native annual grasses such as cheatgrass and medusahead (*Taeniatherum caput-medusea*) persist in cold desert regions like the Great Basin because rainfall is typically sufficient to support reproduction during any given year. Although the fuelbeds they create may only significantly affect fire behavior following years of high rainfall, their populations will likely persist even during years of low rainfall. As a result, non-native grasses and the altered fire regimes they cause are now relatively permanent features in many parts of the cold desert region.

In contrast, the hot desert regions of the Mojave, Colorado, and Sonoran deserts receive less annual rainfall than the cold desert regions, increasing the chances of population crashes of non-native annual grasses such as cheatgrass and red brome (*Bromus rubens*). Rainfall events as small as 5 mm (2 in) can stimulate their germination, and when there is little subsequent rainfall, the plants often die before reproducing (M. Brooks and R. Minnich, personal observations), potentially depleting the soil seedbank. This is probably why red brome became locally extinct at two low elevation desert sites after the late 1980s drought, and at one low elevation site after the late 1990s drought (R Minnich, unpublished data). However, extirpation of red brome did not occur at many higher elevation desert sites following these same drought periods (M. Brooks, personal observation). Broad-scale responses by non-native grasses to droughts indicate that they are typically not regionally extirpated and can recover to ecologically significant numbers relatively quickly in hot desert regions. For example, after the end of the approximately 30-year mid-century drought (Hereford et al. in press) red brome density and biomass jumped 700% and 150% respectively between the last year of the drought (1975) and the first year of higher rainfall (1976), and by 1988 the increase above 1975 levels reached 15,646% for density and 1,596% for biomass at a Mojave Desert/Great Basin ecotone in southern Nevada (Hunter 1991). During this time interval, density and biomass of native annuals decreased (Hunter 1991), while the frequency and size of fires across the Mojave Desert steadily increased (Brooks and Esque 2002,). In addition, the shorter 1987-1991 drought was followed in 1993 by one of the biggest fire years in the 1980-2001 agency fire record for the hot desert regions, and the spread of many of these fires was facilitated by substantial fine fuebeds of red brome and cheatgrass.

Thus, non-native annual grasses will not likely ever become extirpated from the hot desert regions under the current climate regime, although their landscape dominance and effects on fire frequency and behavior will undoubtedly continue to be highly episodic in response to rainfall. Non-native grass/fire cycles have already become established in some localized hotspots within the hot desert region (Brooks and Esque 2002). The extent of area affected by these vegetation and fire regime type-conversions may expand during periods of high rainfall in the future, although most of this expansion will probably be confined to the middle elevation desert shrubland and grassland ecological zone. Below the middle elevation zone, extreme drought conditions will cause more frequent population crashes of red brome and cheatgrass and thus limit their influence on fire regimes, and above the middle elevation zone native woody plants and perennial grasses are the primary factors affecting fire regimes.

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SIDEBAR 16.2. Saltcedar Invasions Can Change Riparian Fire Regimes

by Tom Dudley and Matthew Brooks

Saltcedar (*Tamarix ramossissima*) was brought to North America in the early 1800's by European colonists as a horticultural plant, and by the early 1900's it became widely used to provide windbreaks and erosion control along railways and other erosion-prone sites. Its ability to tolerate periodic drought and harsh soil conditions helped insure its establishment persistence where other species failed. It was recognized as an invader of desert watercourses around the 1920's, and with the advent of water control and diversion projects took advantage of the altered conditions to expand its range during the middle and latter part of the century (Robinson 1965).

Saltcedar is deciduous and produces a fine-structured, water-repellent litter layer that is highly flammable in late summer and fall. Because stand densities can be very high, and litter is slow to decompose, a nearly-continuous layer of surface fuels can develop which carries fire throughout the stand (Busch and Smith 1992). The standing trees are also flammable, and can carry fire from surface fuels up into the canopies of native riparian trees. These fuel characteristics can create a frequent, high intensity, crown fire regime where an infrequent, low to moderate intensity, surface fire regime previously existed. After burning, saltcedar stump-sprouts readily and benefits from nutrients released by fire, whereas native riparian plants such as cottonwood and willow do not resprout as vigorously (Ellis 2001). Recurrent high intensity fire may lead to monoculture stands of saltcedar. Thus, saltcedar has turned many watercourses from barriers of fire movement to pathways for fire spread.

As stands of saltcedar increase in density and cover, native cottonwood and willow trees decrease. In some cases this is coincident with changing environmental conditions that do not favor the native species (e.g. decreased water tables caused by water diversion projects; Everitt 1998), but in other cases it is clear that saltcedar is responsible for the decline in native trees, directly through competition and indirectly through altered fire regimes (Busch and Smith 1995). Because it provides lower quantity and quality of shade, forage, and insect prey species, wildlife generally avoid large stands of saltcedar in preference for native stands (Shafroth et al. in press). This includes numerous threatened and declining riparian birds which find better nesting and feeding resources on native trees. In addition, saltcedar can have higher evapotransporation rates than native trees, potentially reducing water tables (Sala et al. 1996). All of these symptoms of saltcedar invasion have caused major management problems in southwestern riparian ecosystems.

Mechanical and chemical methods are typically used to manage saltcedar, however they can be very expensive ($300 - $6,000/ha.; Shafroth et al. in press), their effectiveness is often limited and temporary, and they can have other undesirable ecosystem effects. After more than a decade of pre-release testing, a leaf-feeding beetle from Eurasia, *Diorhabda elongata*, has been experimentally released in several western states as a biological control agent against saltcedar (Dudley et al. 2000). At one site in northern Nevada this beetle defoliated approx. 2 ha in 2002, and spread to defoliate over 400 ha in 2003. The physiological stress experienced by defoliated plants may lead to lowered live fuel moisture, and definitely increases the amount of dead wood and foliage. In the short term, this biocontrol may increase the chance of high-intensity fire, but in the long run the conversion of saltcedar stands back to native riparian woodlands will likely reduce fire hazards.

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SIDEBAR 16.3. Fire Effects on the Desert Tortoise (Gopherus agassizii)

by Matthew Brooks and Todd Esque

Changing fire regimes threaten 12 of the 40 major tortoise species worldwide (Swingland and Klemens 1989). Only general habitat destruction is listed as a threat for more species (23 of 40 species). In general, tortoises are poorly adapted to fire because they evolved in arid or semi-arid habitats where fire was historically rare. The desert tortoise (*Gopherus agassizii*), Mojave population, is a Federally Threatened species listed partly because of threats posed by fire.

Fires can kill desert tortoises, especially fires that occur in the spring and early summer when they are most active above-ground throughout their range (Esque et al. 2002). Years of high rainfall produce the profuse annual plant growth that is required for desert tortoise reproduction, but it also contributes to fire occurrence, especially at the low and middle elevation zones within the desert tortoise range. Thus, years when growth and reproduction are expected to be greatest can be coincident with increased fire occurrence. Although, mortality from individual fires is generally considered insignificant for wildlife populations compared to the habitat changes that can follow, loss of a few individuals may be catastrophic for local populations of species that are already in decline (Esque et al. 2003).

Fires can also affect desert tortoises indirectly, by changing habitat structure and plant species composition. Loss of cover sites that provide protection from the sun and predators, and loss of native forage plants are specific examples of the potential negative effects of fire (Brooks and Esque 2002, Esque et al. 2002). Individual fires may have relatively small indirect effects within desert tortoise habitat, since they are often patchy, leaving unburned islands of native vegetation. In contrast, recurrent fires pose a much greater threat, as they often burn through previously unburned islands of vegetation, and can produce broad landscapes devoid of shrub cover and dominated by non-native annual grasses. These conditions are currently focused within a number of regional hotspots in the desert bioregion (Brooks and Esque 2002).

When fighting fires that occur within desert tortoises habitat in the low and middle elevation zones, land managers follow guidelines developed to reduce the chance of killing desert tortoises such as not burning out unburned habitat islands when feasible, checking under tires before moving vehicles, and walking ahead of vehicles when they are required to travel off-road (Duck et al. 1998). Results of firefighting activities in desert tortoise habitats have proven that the benefit of fighting fires in desert tortoise habitat far outweighs the potential danger of damage to habitats and tortoise populations when appropriate guidelines are followed (Duck et al. 1998).

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Resident Golden Eagle ranging behaviour before and after construction of a windfarm in Argyll

D WALKER, M MCGRADY, A MCCLUSKIE, M MADDERS & D R A MCLEOD

Resident Golden Eagle ranging behaviour was monitored over 776 observation hours before and after construction of a windfarm in Argyll, western Scotland between 1997 and 2004. Overall size of the eagle range that was potentially affected by the windfarm (for male, female and both eagles) was similar before and after construction. Eagles appeared to change their ranging to avoid the windfarm site. Once built the windfarm was over flown mostly when other eagles intruded on the territory. An area of plantation forestry was felled with the aim of mitigating the potential loss of foraging habitat to the windfarm, and drawing eagles away from the windfarm thereby reducing collision risk. Eagles were seen in the tree cleared area 3 times more often after felling than before felling, and the shift in ranging was away from the windfarm and in the direction of the felled area. These findings are from a single pair and should be used cautiously when applied to other, similar, situations. However, they are an important first step in understanding the likely effects of windfarms on eagles.

Introduction

In the UK in 2004, 253 MW of new, wind generated electricity was added to the national grid, 5 times the annual amount in the 1990s and double the 2003 figure. In Scotland, 11 schemes are under construction and due to come on line by the end of 2005. Many more developments are being planned in Scotland, and 70% of onshore schemes being considered for planning approval in the UK are located there (British Wind Energy Association 2004). Prospecting for new, commercially viable sites continues.

Scotland holds virtually all breeding pairs of Golden Eagles *Aquila chrysaetos* in the United Kingdom. Windfarms located within the range of Golden Eagles can cause eagle deaths due to collisions (Hunt 2002), and it has been thought that eagles may alter their ranging behaviour to avoid turbines, thus rendering the habitat within the windfarm area unavailable to foraging eagles. In Scotland these possible impacts have led to the adoption of a cautious approach to the siting of windfarms with regards to the location of territorial eagles.

A 46 turbine windfarm, the Beinn an Tuirc windfarm, was constructed during 2001 within an occupied eagle territory in Argyll. In addition, another windfarm, the Deucheran Hills windfarm, was built in 2001 (9 turbines) about 6.4 km to the north of the Beinn an Tuirc site, and is more peripheral to the home range of the eagles. To mitigate the potential habitat loss resulting from the Beinn an Turic windfarm, a habitat management plan was implemented that included forest clearance and management of existing Heather (*Calluna vulgaris*) moorland to increase the abundance of potential eagle prey (eg Willow Ptarmigan *Lagopus lagopus scoticus* and Black Grouse *Tetrao tetrix*). The creation of new areas of foraging habitat away from the windfarm was also thought likely to reduce the risk of eagle collisions with the turbines. An on going programme of eagle monitoring was

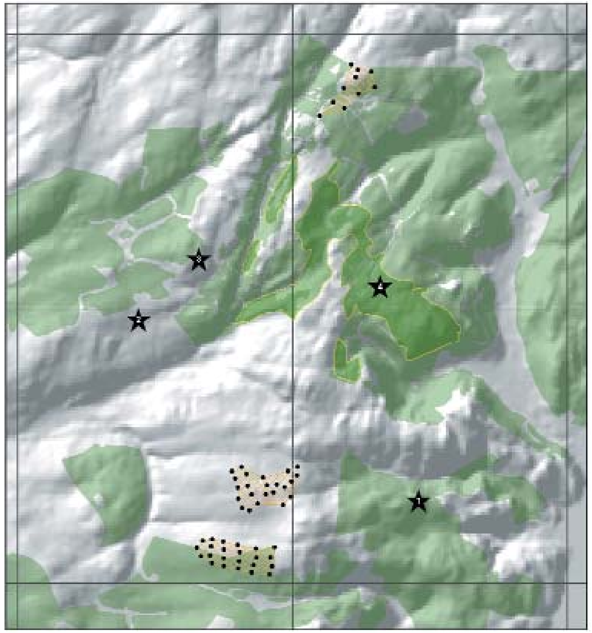
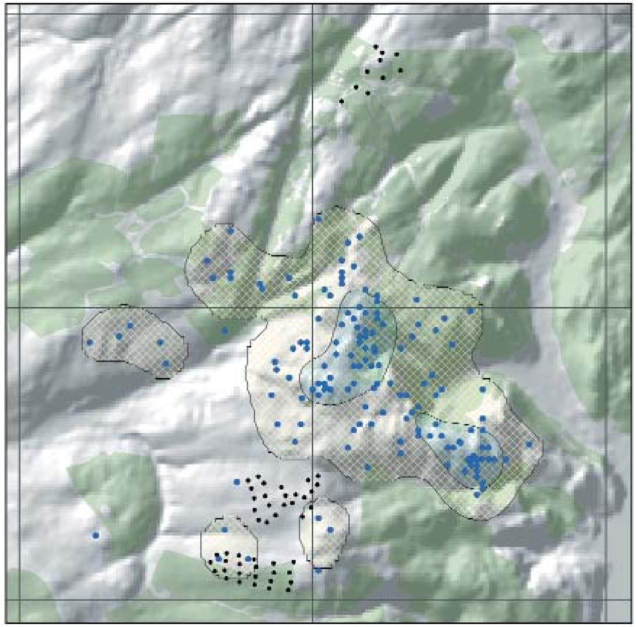


Figure 1 *Study area. Grid lines are 5 km x 5 km.*

Figure 2 *Kernel analysis of resident eagle movement (n=154) 1997-2004.*



undertaken from 1997 to assess effects of the Beinn an Tuirc windfarm and the habitat management plan on Golden Eagle ranging and breeding performance.

The Golden Eagle is a species of medium conservation concern in Britain (Gibbons *et al* 1996). In Argyll habitat changes that adversely influence foraging potential (eg upland afforestation and overgrazing of Heather areas) have affected territories adjacent to the one studied by us (Watson *et al* 1987). In spite of the similar loss of much land to plantation forest within the estimated eagle home range that includes the Beinn an Tuirc windfarm, there remains an extensive area of open land with modest populations of important prey species such as Willow Ptarmigan. Because of this the home range continues to be potentially viable for breeding eagles.

Study area

The Beinn an Tuirc windfarm (255 ha) and eagle monitoring area (ca 57 km^2) straddle the main ridge (Figure 1), which is generally below 300m above sea level, though there are peaks of ca 450m. The eastern slopes of this ridge, to a distance of about 3 km, are characterized by deeply cut valleys, with rock outcrops that provide a number of suitable eagle nest sites. To the west of the main ridge for a distance of about 8 km the terrain is gentler, characterized by wide, rounded ridges and shallow incised stream courses that run to the sea. This east west pattern extends both north and south of the study area.

Landcover within the monitoring area includes commercial forestry blocks, mostly Sitka Spruce *Picea sitchensis* of varying age, and open hill, dominated by grass and Heather; open areas include both grazed and ungrazed habitats, which are mostly acidic grasslands with some areas of shrub heath and areas of blanket bog on the higher slopes. Between October 1999 and June 2001 an area of forest (ca 280 ha) was felled to the north east of the main open area as part of the habitat management plan. Eagle monitoring focused on an area of ca 34 km^2 of open hill, which is bounded on the north and south by forest, but also includes ca 7 km^2 of open ridges within forest blocks to the north.

The diversity of natural fauna is limited, and a number of species, such as Mountain Hare *Lepus timidus* and Golden Plover *Pluvialis apricaria*, no longer occur locally as breeders. Mammals include small numbers of Rabbits *Oryctolagus cuniculus* around the fringe of the monitoring area, occasional Brown Hares *Lepus europaeus* towards its western edge, Sika *Cervus nippon* and Roe *Capreolus capreolus* Deer in the plantations and Foxes *Vulpes vulpes*. The birds are typical of upland areas in western Scotland (Ratcliffe 1990). Birds breeding on or using the area include diurnal and nocturnal raptors, Red-throated Divers *Gavia stellata*, small numbers of Mallard *Anas platyrhynchos*, Eurasian Teal *A. crecca* and Mew Gulls *Larus canus*. The forest avifauna is dominated by passerines such as European Robin *Erithacus rubecula* and Chaffinch *Fringella coelebs*, and corvids *Corvus* spp. Black Grouse are present in 3 to 4 areas of the younger plantations, but also occur on the open hill. The open hill holds a scattered population of Willow Ptarmigan, which are mostly associated with areas of Heather moorland. Small numbers of Common Snipe *Gallinago gallinago* and Eurasian Curlew *Numenius arquata* occur in grass dominated wet flushes.

The Beinn an Tuirc windfarm contains 46 – 660kW turbines that are divided evenly into 2 groups (north and south); within these groups the turbines are > 150 m apart. At its narrowest point the gap between the north and south areas is about 670 m. The Beinn an Tuirc windfarm itself is located in the central southern section of the main block of open area with plantation forestry bordering its southern edge. Some plantation forestry (ca 50 ha) was removed to accommodate the southern section of the windfarm.

Human activity in the study area prior to windfarm construction mostly comprised shepherding on the open hill, deer stalking within the forests and ecological project survey work throughout the area. Forest operations, eg felling and planting, are ongoing, but the location, timing and extent of these are controlled, especially during the breeding season, to lessen potential impact on the eagles. Since construction, regular maintenance of the wind turbines has been added to the list of human activities in the area. Human visitor pressure on the open hill by hill walkers, both before and after construction, was very limited and mostly associated with accessing the highest summit.

Methods

Observations of eagle movements were made from 4 vantage points (VP). From these we monitored range occupancy, habitat use and foraging effort by the individual eagles, and collected information on eagle behaviour. Two VPs have been in use since 1997, a third was added in 1998 and a fourth in 1999. The Beinn an Tuirc windfarm area and main open area have been monitored since 1997; the addition of the last 2 VPs allowed us a better view of an area of forestry felled in mitigation of the windfarm. Collectively, the area viewed from the VPs comprises the eagle monitoring area, and VPs are located around the perimeter of this area so that the greatest continuous panorama is under observation, while reducing any potential influence of observer presence on eagle behaviour.

Observations were made 8 times per year (twice per quarter) from each VP between November 1997 and April 2004 except during March to December 2001, when fieldwork was curtailed by Foot and Mouth Disease access restrictions. Within each quarter all 4 VPs were visited; the order of visits was arbitrary. Weather could affect the area viewed from any particular VP and the duration of any particular watch period. Observation periods were chosen to avoid periods of continuous heavy rain, snow or dense fog, and ideally were 4 hours in length. Where possible, watches affected by poor weather conditions were extended to achieve 4 hours of observation time. While weather conditions could affect VP visibility they did not influence choice of VP, and all VPs were visited in a variety of conditions. While most watches tended to cover the middle of the daylight period, observations occurred at all times of the day. A total of 392 hrs of observation were made before construction, 68 during construction and 316 hrs after construction.

A single, experienced observer (DW) made all observations. The viewing area was kept under continuous observation for the full watch period by above skyline scanning without optical aids, binocular scanning of all areas and regular telescopic checks of known and potential perches. In so doing bias in observer effort towards specific locations within the viewing field was minimized.

When an eagle was seen, the time of first contact was recorded to the nearest second, and the bird's flight path was plotted on a paper map. Simple flights were synchronously plotted in the field, prolonged flights were plotted in sections that were drawn synchronously or nearly so, and fast or short flights were plotted immediately after they occurred. Final plotting of more complex flight lines was completed as soon as was possible after the watch period. In this way a complete activity log of eagle behaviour and location was kept for each VP session. An estimation of altitude above the ground (in range

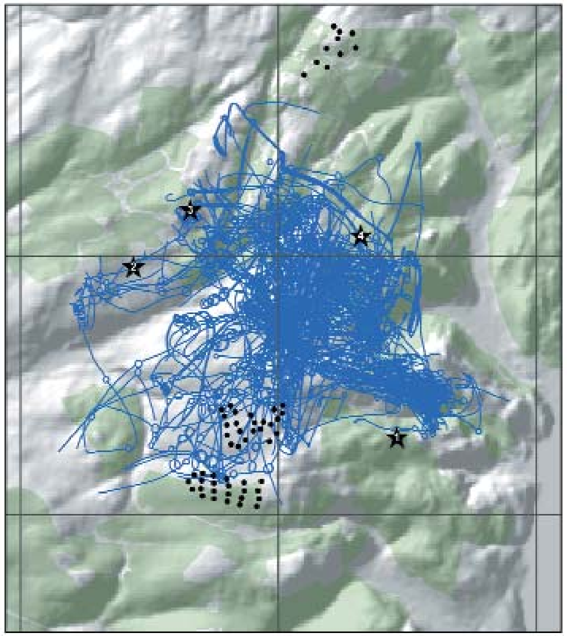
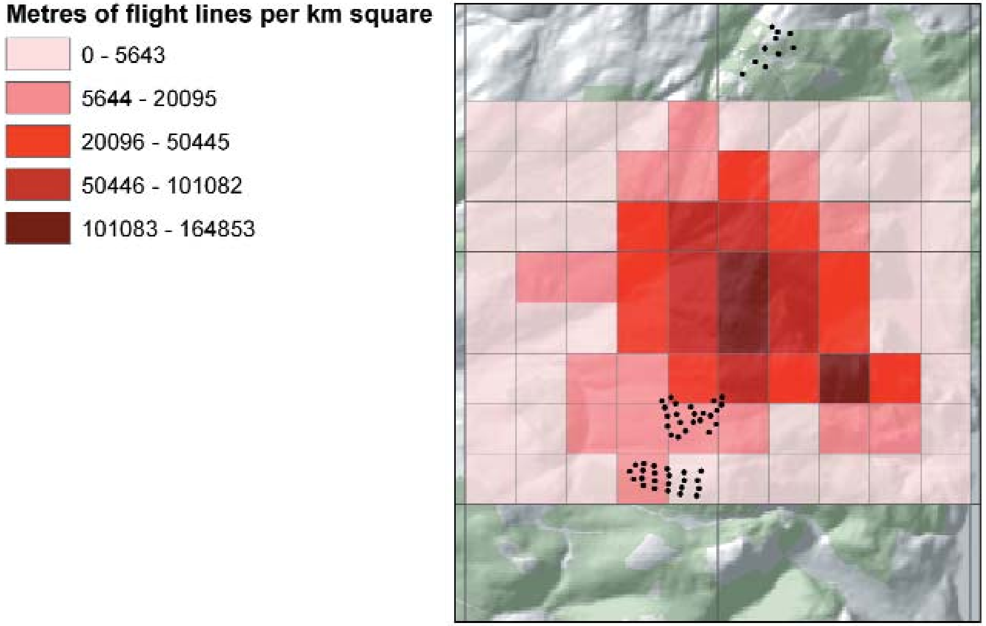


Figure 3 *Flight lines (left, n=811) of resident Golden Eagles (male and female). Grid (1 km^2) colour shows relative use by eagles (dark red=heavy use, light pink=light use).*



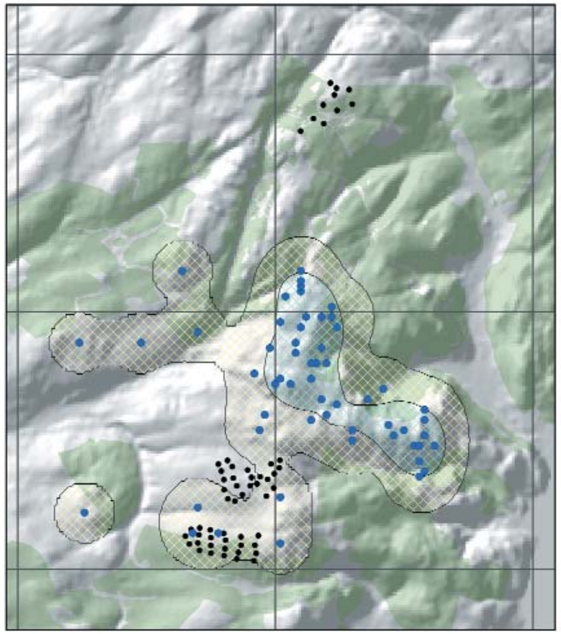
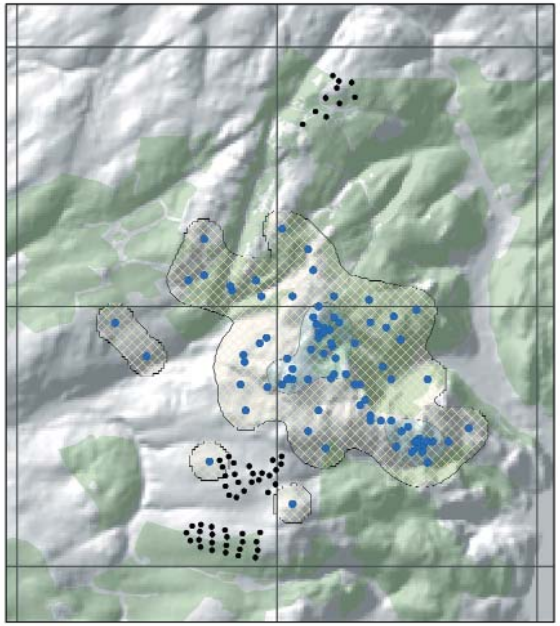


Figure 4 *Kernel analysis of ranging of resident eagles (male and female) showing their ranging before (left, n=57) and after (right, n=83) windfarm construction.*



bands of <5m, 5-20m, 21-60m & >60m) and activity (hunting, transitional flights, species interaction, display, height gain and directional flights) were noted to the nearest second, as was the time when the bird either landed or flew from view. Factors that might influence eagle behaviour (eg human activity, presence of intruding eagles) were also noted. Even when more than one eagle was visible, all flights were followed, timed and plotted. No flights were excluded from the recording process and no assumptions were made about the route or activity of birds when they were intermittently lost from view.

Analyses of eagle ranging data

Two analytical approaches were taken, one based on generating a representative set of eagle locations and one that used a grid overlaid on eagle flight lines to calculate an index of use of km^2 areas by eagles. These were used to create maps that show location, extent and concentration of use by eagles. Data on eagle ranging and habitat were entered into a Geographical Information System (GIS, ArcView 3.3 and ArcGIS, ESRI, Redlands, CA, USA), where analyses and map making were undertaken using the Animal Movement (ver 2.0) extension (Hooge and Eichenlaub 1997).

Point analysis. We framed the area in which eagles were observed by mapping the maximum extent convex polygon, the vertices of which were the most outlying of observations of eagles. The maximum extent convex polygon probably overestimates the actual range, so we also used a randomised selection of points along mapped flight lines to generate a 'representative' set of eagle locations that could be analysed. Points along plotted flight lines were selected in a way that promoted randomness and independence, while enhancing sample size. To do this we randomly selected a single point along the flight lines for each 4 hour observation bout, then selected the sequence of points before and after that random point that were separated from that point and from each other by at least 45 minutes. Observations of radiotagged, territory holding eagles in western Scotland suggested that they can fly from one end of their range to the other in < 15 minutes (McGrady unpublished data), so the 45 minute limit we set is a conservative estimate of the time needed to achieve independence between points. These randomly selected eagle locations were then used to produce maps of area use for the resident male eagle, for the resident female eagle, and for the eagles as a pair. Two representations of eagle range use were employed that used randomised point data: the minimum convex polygon (MCP) (Mohr 1947) and an adaptive kernel analysis set at 95 and 50% levels (Worton 1989). The MCP maps extent of the random location's distribution and kernel analyses map likely use of areas by eagles based on the distribution of eagle locations over time. The 50% kernel predicts the centrally located area where eagles concentrate 50% of their time, and is used by us as a nominal "core area".

One to 6 observations of intruding eagles were made per year. These are not included in our analyses, but provide useful context for interpreting behaviour of the resident eagles.

Grid analysis. The study area was overlaid with a grid that corresponded to the Ordnance Survey one km grid. We then measured the total length of flight lines recorded from our direct observations that occurred in each square. Total length of flight lines per grid square was then mapped and used as a measure of eagle use.

We made comparisons of ranging before (prior to August 2000) and after (after January 2002) windfarm construction for the male, the female and the pair using the kernel analyses and the flight line information. By way of these comparisons we assessed the effect of the Beinn an Tuirc windfarm and the effects of the associated tree felling and habitat management. Because data are from eagles within a single range, and likely to be the same individuals, robust statistical analyses could not be undertaken.

Results

A total of 776 observation hours were logged over 194 watches. Prior to construction 98 watches were made, during construction 17 watches, and after construction 79 watches. No eagles were seen during 60 of the watches.

Golden eagle occupancy and breeding

The home range was occupied throughout the study period, apparently by the same 2 adult eagles. The eagles used a different nest in each year until 2003 when that of 1998 was reused. The eagles laid 2 eggs each year except 2003, when a single egg was laid. A single juvenile was fledged in 1997. During the study period, productivity was 0.125 young per breeding attempt.

Golden eagle ranging

The maximum extent convex polygon in which eagles ranged covered 49.2 km^2; the MCP covered 32.9 km^2 (n= 154). Thirty two percent of the Beinn an Tuirc windfarm was overlaid by maximum extent convex polygon and 28 % was overlaid by the MCP. The 95% kernel of eagle ranging covered 20.5 km^2, and had 2 core areas (50% kernel) that were both outside the Beinn an Tuirc windfarm area and covered a combined area of 2.9 km^2 (Fig 2). The windfarm area was only overlapped by the 50-95% isopleth of kernel analyses of eagle ranging ie it was not included in the core area. Table 1 summarizes the areas of 95% and 50% kernels of eagle home ranging before and after construction and the amount of overlap between eagle ranging maps and the footprint of the Beinn an Tuirc windfarm. Eagle ranging kernels are illustrated in Figures 2-4.

Three randomised locations of eagles (2.56% of all locations) were over the windfarm footprint, two (1.7%) were over turbines, and all of these were prior to construction. Additionally, 3 locations were within 500 m of the windfarm and 2 of these were prior to construction.

Kernel areas for males were similar to those of females (Table 1). Also, for both sexes kernel areas were similar before and after windfarm construction, though the shape and spatial location of the ranges shifted, mostly east and north (Figures 5 and 6) after construction.

Table 1 ***Areas (km^2) within 50% and 95% kernels for eagles during the whole study period and before and after windfarm construction. Values in () are % of eagle range that overlap the windfarm.***

	N	50% area kernel	50-95% kernel	Total 95% kernel
Male 97-04	66	3.0 (0)	17.8 (4.4)	20.8 (3.8)
Male pre construction	27	6.1 (0)	19.3 (6.7)	25.4 (5.1)
Male post construction	37	2.3 (0)	15.0 (0.03)	17.3 (0.03)
Female 97-04	88	4.9 (0)	20.8 (3.7)	25.7 (3.0)
Female pre construction	30	4.7 (0)	20.6 (8.9)	25.3 (7.2)
Female post construction	46	3.8 (0)	19.7 (2.4)	23.5 (2.0)
All birds 97-04	154	3.2 (0)	20.9 (2.7)	24.1 (2.4)
All birds pre construction	57	5.2 (0)	20.7 (9.0)	25.9 (7.2)
All birds post construction	83	6.9 (0)	33.6 (0.5)	40.5 (0.4)

Figure 5 *Kernel analysis of ranging of resident male eagle before (left, n=27) and after (right, n=37) windfarm construction.*

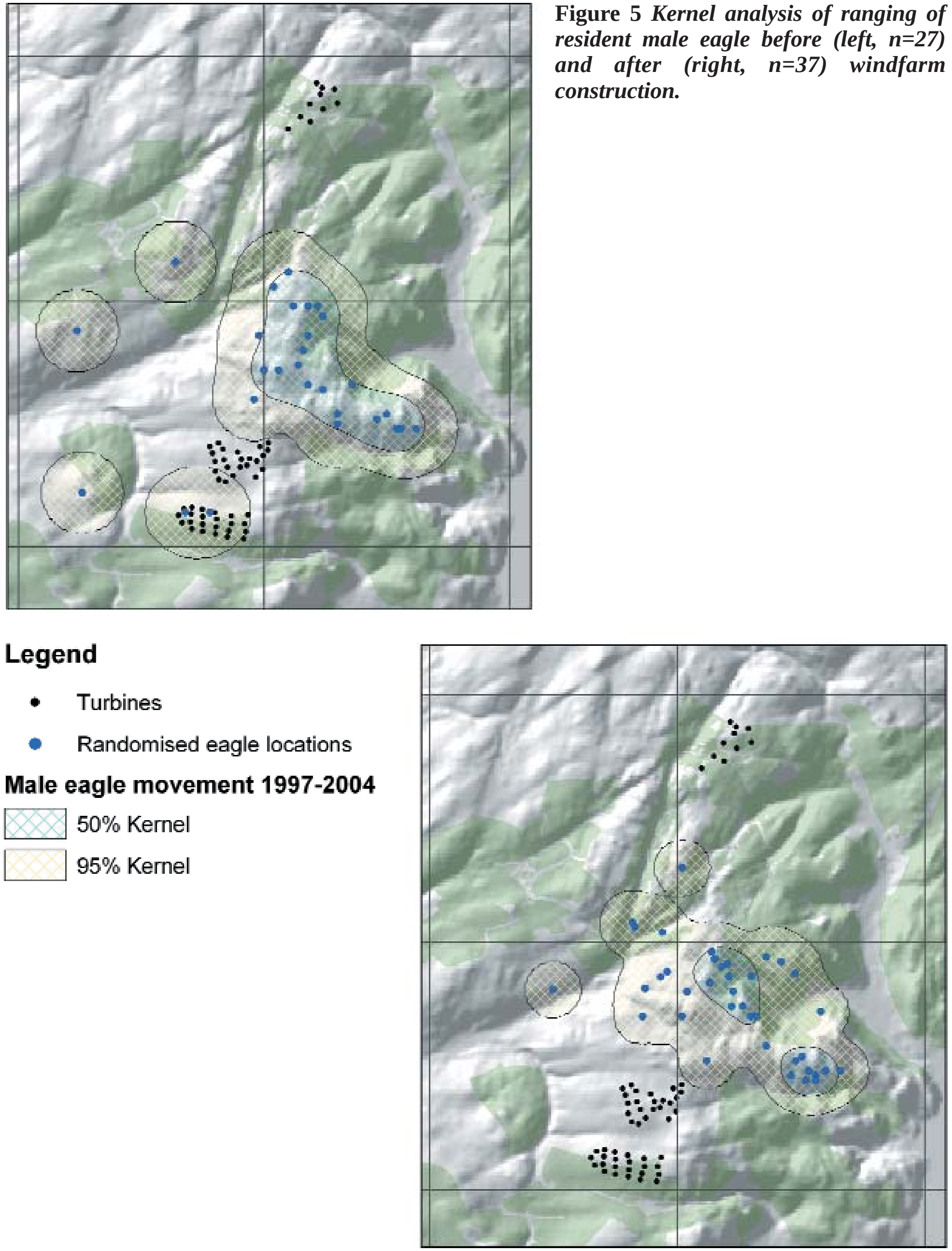
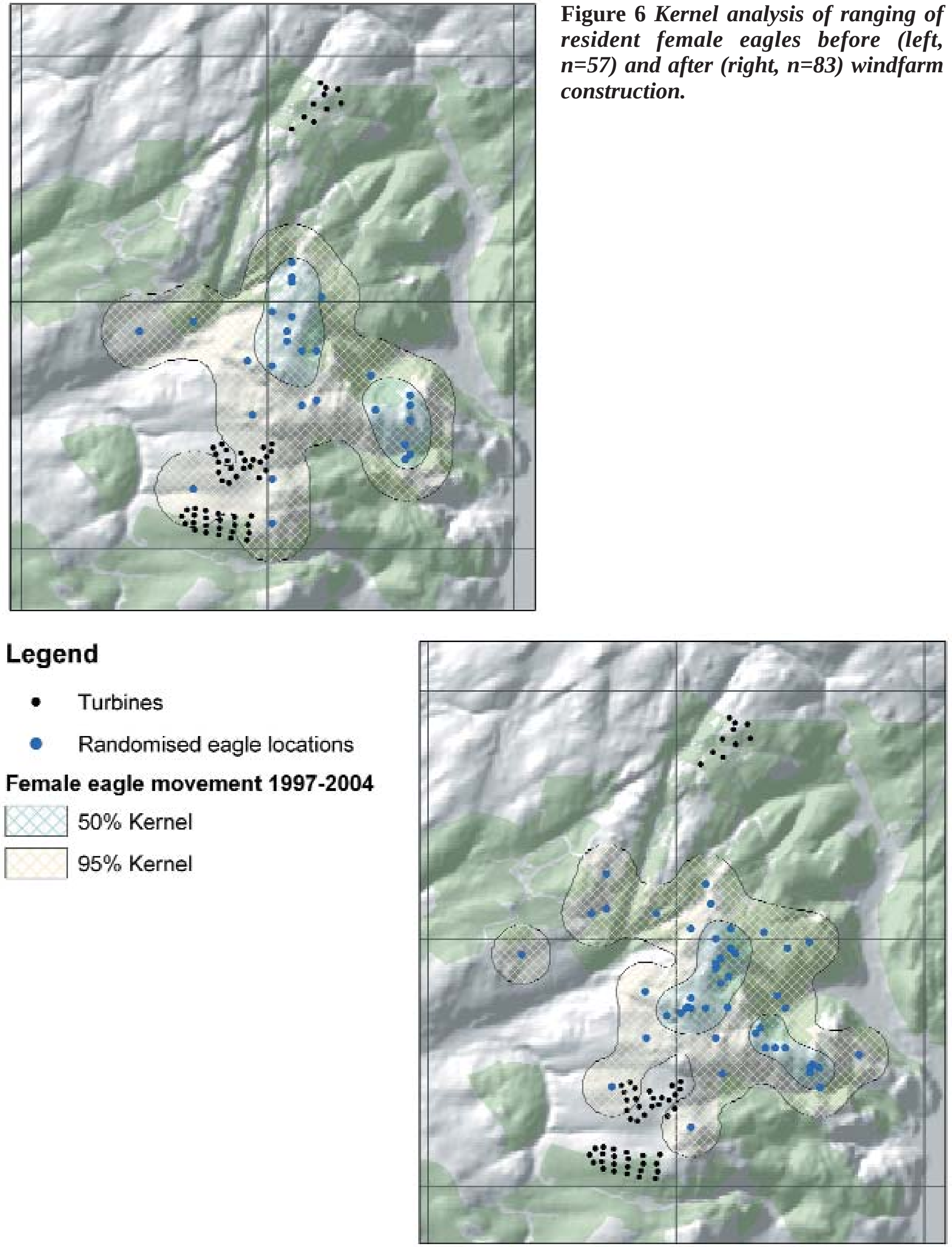


Figure 6 *Kernel analysis of ranging of resident female eagles before (left, n=57) and after (right, n=83) windfarm construction.*



A total of 811 flight paths were mapped. Only one eagle flight line was recorded at low to medium altitude (21-60 m) within the Beinn an Tuirc windfarm after construction and this passed between the 2 discrete clusters that comprise the windfarm. In that instance the nearby presence of an intruding eagle was almost certainly a contributing factor. No eagles have been seen within the turbine clusters. Two of 3 instances of eagles over flying the windfarm were when intruding eagles were in the area.

Seventy seven percent of randomised locations were over open landcover types. The percentages of locations over different landcovers suggest the following ‘preference’ by the eagles: heather moor>treefell>grass hill>forest. Eighty percent of pre construction randomised locations were over open landcover types; the value was 79% for the post construction period.

Regarding the area of forestry that was felled, 21.6% of random locations prior to felling (n=37), 3.1 % of random locations during felling (n=32), and 18.8% of random locations after felling (n=85) were within this area. Eagles flew 0.095 km over the forest area prior to felling per hour of observation and 0.285 km/hr of observation after felling, a three-fold increase in use. Figure 8 utilizes flight line data and shows relative use of different areas overall and proportion of use of each habitat polygon before and after tree felling. Over 70% of total eagle flight line length was over the central open area. Figure 8 illustrates that eagles shifted their ranging to the northeast after trees were felled.

Discussion

Impacts of windfarms on birds can include collisions (See Hunt *et al* 1999 and Hunt 2002) or loss of habitat (eg Leddy *et al* 1999). In this study, resident Golden Eagles appeared to avoid the windfarm within their home range except when responding to intruders south and west of the centre of the territory. Studies exist that show that birds (eg Osborn *et al* 1998) including raptors (Curry and Kerlinger 1998) will try to avoid moving turbines.

Physical accessibility does not seem to be what hinders eagle use of the windfarm. Turbines were separated by relatively large distances, larger than tree spacing in forested areas used by Golden Eagles (Tjernberg 1983), and the eagles we studied were seen hunting Willow Ptarmigan in open patches and rides within forestry smaller than those available within the windfarm (D Walker unpublished data). In combination with the fact that resident eagles continue to forage in areas comparatively close to the windfarm especially toward the centre of the range this suggests that eagles avoid the windfarm as a unit rather than individual turbines. While food densities are comparatively low within the windfarm footprint, current potential prey populations of Willow Ptarmigan, Common Snipe and sheep carrion (S Sheridan and D Walker, unpublished data) and previous use suggest that the eagles would still forage within the windfarm area if turbines were not in place. In particular, eagle foraging might be expected here at times of relatively high grouse availability, July-October, but this has not been recorded since construction. Also, the regular presence within the windfarm of corvids, upon which eagles prey, suggests that eagles may be excluded from the windfarm. Hooded Crows *Corvus corone cornix* are a comparatively common and easily taken prey species but appear to be safe from predation while within the farm. Rotor noise and movement or prey distribution, or any combination of these factors, may be influencing eagle movement. However, we had no impression that the windfarm was avoided less during periods when the turbines were not rotating (D Walker, unpublished data).

The kernel map of eagle ranging suggests that the windfarm may act as a barrier to some areas of the range for the eagles, however VP watches prior to construction did not suggest that the windfarm footprint was along any major transit route for the eagles.

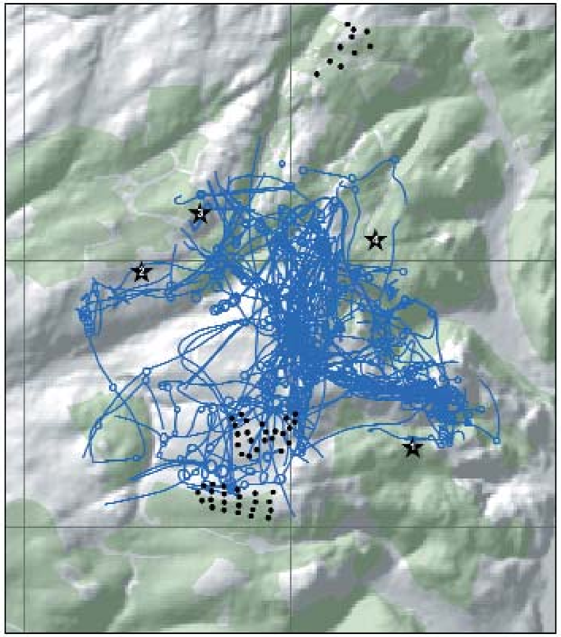
The management plan for this windfarm included activities that potentially would reduce risk of collision by reducing prey availability within the windfarm. In addition, the enhancement of other areas for eagle prey was seen as providing new feeding opportunities for eagles. According to the grid based analysis eagles did appear to more frequently use an area where trees were felled to improve foraging potential. The random point analysis did not show this, though low sample size in the pre felling period could have caused this. Willow Ptarmigan numbers have increased here (S Sheridan unpublished data) since felling, and use of the area by eagles may increase further as prey numbers recover from being limited by blanket forest and their availability increases. This may further reduce the relative attractiveness of the land within and around the windfarm to eagles.

The relative use of different habitats by the eagles to some extent reflects their foraging potential. However, even within particular habitat types there can be variations in quality and prey carrying capacity. Still, so far the findings point to the Golden Eagles at Beinn an Turic being similar to eagles elsewhere and preferring open habitats to closed ones (McGrady 1997, McGrady *et al* 1997). In contrast, eagle use has increased in areas where managed tree felling occurred. The area where trees have been felled in mitigation of open ground lost to the windfarm notwithstanding, tree growth to canopy closure in other areas will restrict use by the eagles. McGrady *et al* (1997) show that eagles avoid areas of closed canopy forestry, probably because prey becomes less available.

Our impression from direct observations of eagles and cursory examination of pellets suggest that the eagles’ most important food source is sheep carrion. It also appears that carrion availability varies spatially and temporally. Carrion hot spots are located in wet flushes on the eastern sloping open ground and the windfarm area, but there was no evidence of use of carrion within the windfarm area by eagles since construction. Most sheep carcasses are removed from the windfarm area when they are found, but some are not found and these have not been used by eagles (D Walker unpublished data). Carrion availability within the windfarm area has probably declined since construction. Rabbits, Willow Ptarmigan and Hooded Crows are the main live prey species we have recorded. This prey list is similar to that recorded for eagles elsewhere in western Scotland (Watson *et al* 1993).

Increased human activity can influence eagle behaviour (including breeding and foraging behaviours) and productivity (Watson 1997), and in general, eagles tend to avoid human activity. We have no data to suggest that increased visitor pressure has caused the eagles to change their ranging behaviour. Indeed, eagles did not go into the windfarm even when no people were there. However, we were unable to monitor eagle ranging at the site during construction when human activity was greatest because of access restrictions due to Foot and Mouth Disease. The windfarm is regularly visited by turbine technicians, shepherds and eagle project and other fieldworkers. None of these activities seem likely to cause reduced eagle use because they tend to be localised and relatively infrequent. It is possible that eagles are influenced more by human activity in artificial habitats (eg windfarms or newly felled forestry) than in natural habitats, but we know of no data to support this.

Figure 7a *Flight paths (left), and grid of relative use of km squares (right) by Golden Eagles (male and female) before windfarm construction at Beinn an Tuirc.*



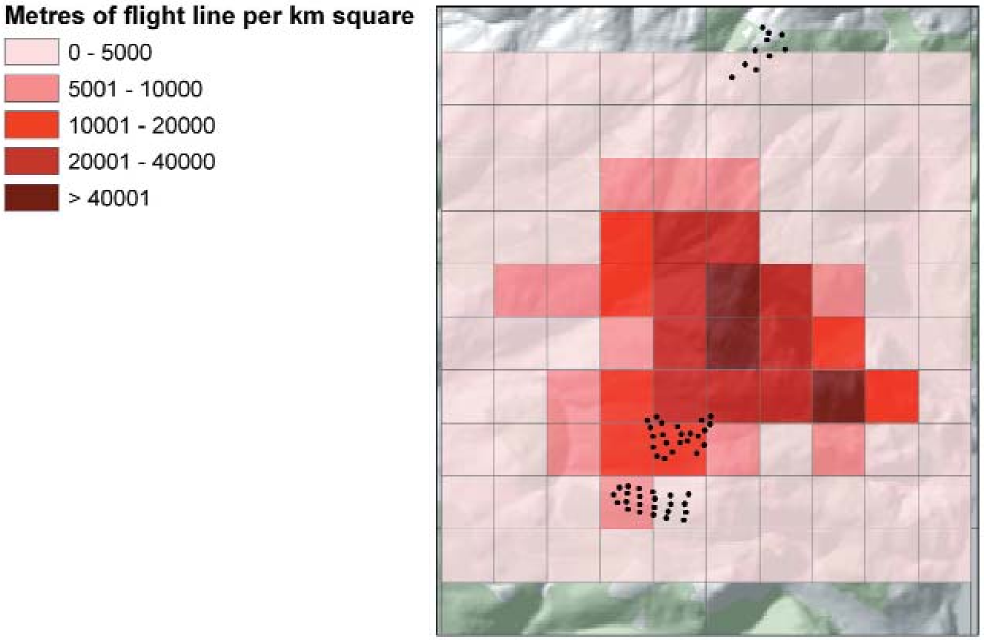
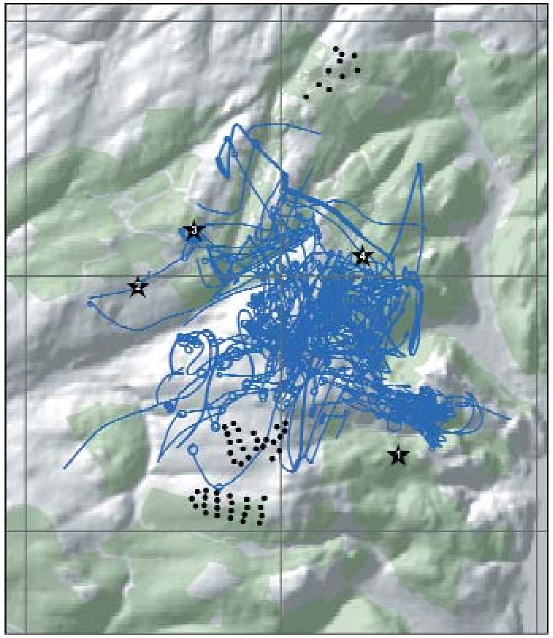
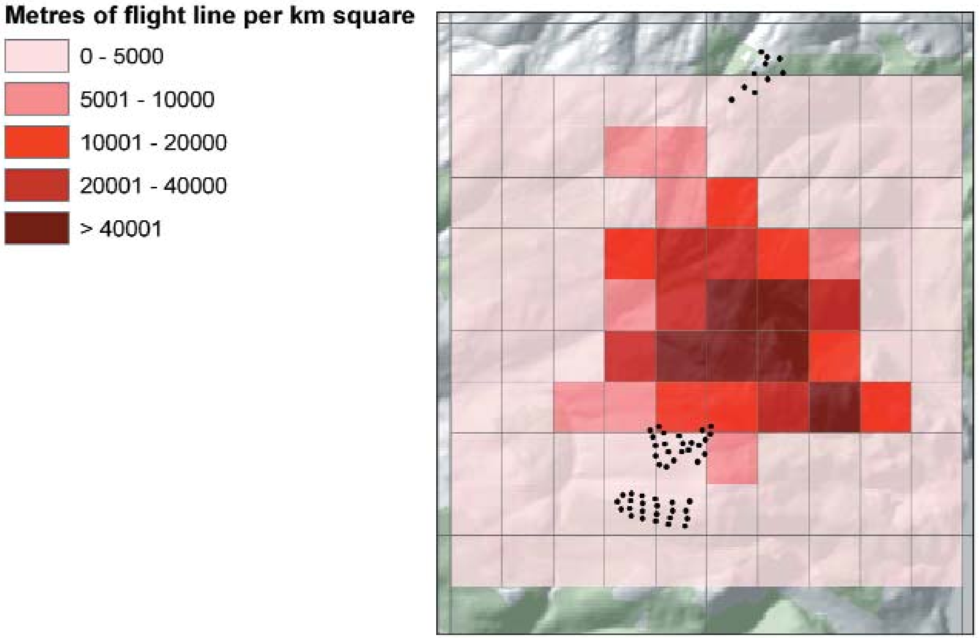


Figure 7b *Flight paths (left), and grid of relative use of km squares (right) by Golden Eagles (male and female) after windfarm construction at Beinn an Tuirc.*





Intruding eagles were mostly recorded outside the breeding season over the main area of open ground and the tree felled area (D Walker unpublished data). When detected, the resident pair routinely intercepted intruding birds, even when they were towards the fringe of their range, with interactions usually consisting of the resident pursuing the intruder, sometimes with apparently aggressive approaches. In general locations away from the territory centre were associated with territorial defence behaviour, especially by the male (eg Figure 5, western edge of left map), and these added greatly to the size of the range that we mapped.

Different methods used to map animal movements have different advantages and shortcomings (Kenward 1987). We present different mapped representations of the same data to partially overcome this problem. Also, although these data are from a single pair, the number of observations (811 flight lines) is large, is spread over different seasons over 7 years, and this lessens the impact of the shortcomings of the range mapping methods.

Golden Eagle occupancy has not changed during the study period. Overall productivity of this range is 0.44 young per attempt (n=28, M Gregory, unpublished data), compared to an Argyll mean of 0.66 (1992, 96, 99-2004, Argyll Raptor Study Group, unpublished annual report 2004) and a Scottish mean of 0.52 (Watson 1997). Although productivity during the project was only 0.14 young per attempt, there is no evidence that links this low reproductive rate to windfarm construction or operation activities. Declines of this magnitude have been recorded in other ranges in Scotland where no windfarm, or indeed other change, has occurred, though we know of no published information that illustrates this. Rather, it seems that this home range has been relatively unproductive in recent years (only one chick since 1988), and this may be a result of the range viability already being challenged by the expansion of forest (Watson *et al* 1987) and the impoverishment of the flora and fauna that has occurred (Thompson *et al* 1995). We have verified the presence of the adult territorial eagles every 2 weeks, and no eagles, territorial or non territorial, are known to have been killed by colliding with the turbines. There is no indication that the resident eagles have become accustomed to the windfarm area and are more likely to use it as time passes. It remains likely that any fledglings reared at the site, intruders, or new 'naïve' replacement breeders are at greatest risk of collision.

Because tree clearance roughly coincided with the construction of the windfarm, it is difficult to say to what extent eagles responded to the clearance rather than the windfarm. However, the avoidance of the windfarm since construction suggests that the existence of relatively open areas within the windfarm is not sufficient motivation to attract eagles for foraging. Further, if the shift to the north east is a result of windfarm avoidance, then it suggests the eagles, at least at Beinn an Tuirc, 'prefer' recently felled forest areas to the windfarm.

Interestingly, though there was an overall shift to the northeast, there was no real shift in the location of the core areas. These remained in the open area that has never been under forestry to the northeast of the windfarm between blocks of forestry. This result is likely influenced by the location of the nest sites, but supports the idea that these areas are particularly important. If this relative inflexibility in location of the core area is a feature of eagles elsewhere identifying the core area and protecting it may be particularly important. Guidance by Watson *et al* (1987) and modelling of eagle ranging (McGrady *et al* 1997, McLeod *et al* 2003a, 2003b) have established nominal core areas for eagles, but these are criticised as being too simplistic, and are a point of contention between developers, conservation organizations and government agencies. More data are needed to clarify the impact of windfarms on eagles, and it would be useful if data collected at windfarm sites elsewhere in Scotland were made available for collective analyses.

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The authors would like to thank Mike Gregory and the Argyll Raptor Study Group for use of data on eagle productivity. Scottish Power funded data collection. Saya Sheridan provided information on habitat and prey within the windfarm management area. Steph Carey-Miller of Natural Research (Projects) provided GIS support. The Central Kintyre Management Group has provided a forum for interesting discussions on windfarms and their effects on eagles, and encouraged us to publish the results.

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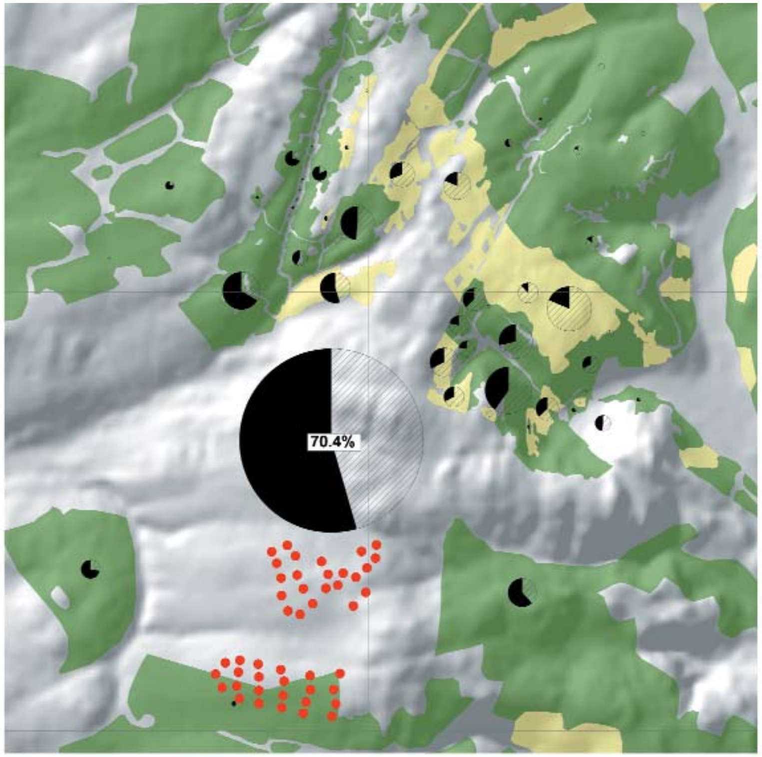

Figure 8 ***Use of habitat by Golden Eagles at Beinn an Tuirc. Size of pie chart shows relative use of habitat polygons for the whole study period, dark portion is percentage use before tree felling, and hatched portion is percentage use after tree felling.***

Relative habitat use
before and after tree felling

◐

▨ Post-felling
■ Pre-felling

● Turbines
🟩 closed canopy
🟨 recent felling, including mitigation felling

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Anthropogenic Degradation of the Southern California Desert Ecosystem and Prospects for Natural Recovery and Restoration

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ABSTRACT / Large areas of the southern California desert ecosystem have been negatively affected by off-highway vehicle use, overgrazing by domestic livestock, agriculture, urbanization, construction of roads and utility corridors, air pollution, military training exercises, and other activities. Secondary contributions to degradation include the proliferation of exotic plant species and a higher frequency of anthropogenic fire. Effects of these impacts include alteration or destruction of macro- and micro-vegetation elements, establishment of annual plant communities dominated by exotic species, destruction of soil stabilizers, soil compaction, and increased erosion. Published estimates of recovery time are based on return to predisturbance levels of biomass, cover, density, community structure, or soil characteristics. Natural recovery rates depend on the nature and severity of the impact but are generally very slow. Recovery to predisturbance plant cover and biomass may take 50–300 years, while complete ecosystem recovery may require over 3000 years. Restorative intervention can be used to enhance the success and rate of recovery, but the costs are high and the probability for long-term success is low to moderate. Given the sensitivity of desert habitats to disturbance and the slow rate of natural recovery, the best management option is to limit the extent and intensity of impacts as much as possible.

> We've mined it, dammed it, irrigated it, developed it, and subjected it to nuclear assault, yet the desert, somehow both fragile and tough, manages to endure, a rugged old touchstone for us to measure ourselves against.
>
> Malcolm Jones, Jr., 1996

The landscape and native vegetation of the southern California deserts have been significantly altered during the last century by a variety of factors including: livestock grazing (Bentley 1898, Humphrey 1958), introduction of exotic species (Mooney and others 1986, Rejmánek and Randall 1994), off-road vehicle use (see reviews in Webb and Wilshire 1983), urbanization and its attendant effects (Reible and others 1982, Walsh and Hoffer 1991), and military activities (Lathrop 1983a, Prose and others 1987). Extreme temperatures, intense sun, high winds, limited moisture and the low fertility of desert soils make natural recovery of the desert very slow after disturbance (Bainbridge and Virginia 1990). Conditions suitable for plant establishment occur only infrequently and irregularly, and it may take hundreds of years for full recovery to take place without active intervention. Many of the actions of desert development and utilization have profound effects on ecosystem stability, diversity, and productivity (Rundel and Gibson 1996).

KEY WORDS: Mojave Desert; Colorado Desert; California; Human impacts; Recovery; Restoration

The literature on human impacts to the biotic and physical components of the Mojave Desert is large and diffuse. In this paper we review the major human-induced impacts on the California desert, and the prospects for natural recovery and restoration, by characterizing the effects of past actions on the Mojave Desert ecosystem and other arid lands. In addition, we briefly suggest practical strategies and methods for planning and implementing desert restoration projects and improving recovery of these areas by soil management, transplanting, direct seeding, and other techniques.

Area of Study

Our review focuses on the Mojave and Colorado Deserts of southern California, an area of approximately 10 million ha. The Mojave Desert occupies portions of Inyo, Kern, Los Angeles, Riverside, and San Bernardino counties in California. The geographical and ecological boundaries of the Mojave Desert are

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discussed in detail by Vasek and Barbour (1977) and Hickman (1993). The modern plant community of the Mojave has been characterized as ‘‘desert scrub’’ (Turner 1982, Hickman 1993), even though it is composed of several recognizable community types including: creosote bush scrub, saltbush scrub, shadscale scrub, blackbush scrub, and Joshua tree woodland (Vasek and Barbour 1977). Perennial plant diversity is low compared to the Colorado Desert: areas dominated by *Larrea tridentata* and *Ambrosia dumosa* occupy about 70% of the Mojave (Lathrop and Rowlands 1983). More than 250 species of annual plants are found in the Mojave, including 80–90 species that are endemic (Turner 1982). In Death Valley and the Salton Sink, annuals account for 42% and 47% of the local flora, respectively (Johnson and others 1978). Overall plant diversity is low below 1000 m, but increases to levels approaching more temperate habitats at higher elevations (Cody 1986).

The Colorado Desert is that part of the Sonoran Desert found mostly in Imperial and Riverside counties, California (Burk 1977). The Colorado Desert is generally separated from the Mojave Desert to the north by the Little San Bernardino, Cottonwood, and Eagle Mountains. The boundary between the two desert ecosystems is poorly defined to the east of these mountain ranges (Vasek and Barbour 1977). A bimodal rainfall pattern composed of winter frontal systems and summer convectional storms distinguishes the Colorado Desert from the western Mojave Desert (Burk 1977), where most precipitation comes from winter rains. In addition, the region is generally lower, flatter, hotter in the summer and warmer in the winter, and hosts a slightly different flora than the Mojave Desert (Hickman 1993). Dominant vegetation in the Colorado Desert is ‘‘Sonoran creosote–bush scrub’’ (Hickman 1993). Plant communities recognized by Burk (1977) include creosote bush scrub, cactus scrub, wash woodland, palm oasis, saltbush scrub, and alkali scrub. There is broad overlap of plant species between the Mojave and Colorado Deserts, but there are a significant number of freeze-sensitive arboreal species that are found only in the Colorado Desert.

Both deserts are characterized by dominant perennial plant species that are long-lived (Bowers and others 1995), some exceptionally so (Vasek 1980). Density and cover of long-lived species increases with age of the site surface (Webb and others 1987, 1988, Bowers and others 1997).

While our focus is specifically directed to the problems of desert lands in California (most of our experience is in the Colorado Desert), we believe our review will prove useful for desert management in other parts of the Southwest, northern Mexico, and in other drylands around the world.

Factors Contributing to Habitat Degradation

The following sections summarize major anthropogenic degradation factors in the southern California desert ecosystem other than agricultural development and urbanization. An understanding of the nature and the effect of disturbances is useful in estimating recovery times or determining what course of action may be required to restore a habitat. Table 1 summarizes the estimated time intervals required for affected plant communities to fully or partially recover from human-induced disturbances.

Impacts on the desert can be loosely divided into historic and current impacts. There is rarely a complete distinction between the two but, in general, the historic impacts include such things as overgrazing, aqueduct building, and the operation of the Desert Training Center in World War II. Grazing still continues, but the major impacts from grazing occurred in the mid to late 1800s. A very rough estimate of the magnitude and extent of these different activities is shown in Table 2. The following factors are not presented in order of importance.

Livestock and Grazing

Cattle and sheep have grazed almost continuously through large areas of the region from the mid-1800s to the present, although the numbers have dropped off in recent years. The establishment of ranching fostered the development of a major industry in the western United States that prospered until droughts, harsh winters, and overgrazing caused a series of dramatic herd declines in the late 1800s. Populations of sheep (60,000) and cattle (67,000) peaked in Imperial County in 1920. In 1968 there were 25,000 cattle and 138,000 sheep grazing on Bureau of Land Management (BLM) and National Monument desert lands in California, predominantly in the Mojave (Ruch 1968). In 1979, 1.8 million ha of public lands administered by the BLM in the California desert were grazed by 75,000 sheep and 14,000 cattle (Bureau of Land Management 1980). Excellent histories of grazing in the desert southwest are provided by Humphrey (1958, 1987).

No published studies have yet fully documented the impact of grazing by livestock in the California desert or estimated the time required for heavily grazed areas to recover to pregrazing levels of plant diversity, density, and cover (Oldemeyer 1994). The rarity of undisturbed reference sites and long-term studies makes it difficult to quantify the effects of grazing, but it is possible to

Table 1. Estimated natural recovery times in years for California desert plant communities subjected to various anthropogenic impacts

Impact	Location	T_{recovery}	Reference
Tank tracks (military)	eastern Mojave	65,[a] 76[b]	Lathrop (1983a)
Tent areas (military)	eastern Mojave	45,[a] 58[b]	Lathrop (1983a)
Dirt roadways (military)	eastern Mojave	112,[a] 212[b]	Lathrop (1983a)
Tent sites (military)	eastern Mojave	8–112[c]	Prose and Metzger (1985)
Tent roads (military)	eastern Mojave	57–440[c]	Prose and Metzger (1985)
Parking lots (military)	eastern Mojave	35–440[c]	Prose and Metzger (1985)
Main roads (military)	eastern Mojave	100–infinity[c]	Prose and Metzger (1985)
Military	eastern Mojave	1500–3000[d]	Prose and Metzger (1985)
Townsites	northern Mojave	80–110,[e] 20–50,[b] 1000+[f]	Webb and Newman (1982)
Pipeline	southern Mojave	centuries[g]	Vasek et al. (1975a)
Powerline	southern Mojave	33[h]	Vasek et al. (1975b)
Fire	western Colorado Desert	5[b,i]	O'Leary and Minnich (1981)
Off-road vehicle use	western Mojave	probably centuries	Webb et al. (1983)
Pipeline (berm and trench)	Mojave Desert	100[j]	Lathrop and Archbold (1980b)
Pipeline (road edge)	Mojave Desert	98[j]	Lathrop and Archbold (1980b)
Powerline pylons and road edges	Mojave Desert	100[j]	Lathrop and Archbold (1980b)
Under powerline wires	Mojave Desert	20[j]	Lathrop and Archbold (1980b)

[a] Recovery time to control density.

[b] Recovery time to control cover.

[c] Estimated recovery time for *Larrea tridentata* to reach control densities.

[d] Estimated recovery time (''if at all'') for recovery to original vegetative structure assuming establishment of control densities.

[e] Compaction recovery time.

[f] Total estimated recovery time.

[g] 30–40 years assuming linear rates of succession; 3000 years until formation of large creosote clonal rings.

[h] Incomplete recovery time in areas of high impact.

[i] Time for appearance of perennial seedlings. See Brown and Minnich (1986) in section on fire.

[j] Biomass recovery assuming that successional vegetative growth is approximated by a straight line. Recovery of long-lived species is estimated to take at least three times longer than indicated.

Table 2. Adverse impacts on California desert, their relative intensity and historical occurrence

Impact	Intensity	Current / historic
Grazing	moderate	primarily historic
Removal of native people	moderate	historic
Invasive plants	moderate / severe	historic / current
Highways	severe	current
Urbanization	severe	current
Off-road vehicles	severe	current
Agriculture	severe	both
Military operations	severe	both
Mining	locally severe	both
Linear corridors	locally severe	current

describe the nature of these impacts and their probable extent. Consequently, conclusions about the effects of grazing on arid ecosystems have been contradictory and controversial (Anonymous 1991, Borman and Johnson 1990, Coe 1990, Field 1990, General Accounting Office 1992, Gillis 1991, Poling 1991). Some argue that grazing is beneficial to rangelands, suggesting that the act of grazing stimulates new plant growth (Savory 1988). Other putative positive benefits include the dispersal of seeds, production of fertilizer in the form of excrement, and churning of soil generated by moving hooves (but see Balph and Malecheck 1985). Others point to negative impacts of grazing including: soil compaction and increased erosion, trampling of plants, and overcropping. Grazing effects on arid ecosystems are reviewed in detail by Archer and Smeins (1991).

The effects of overgrazing are far less controversial. As early as the late 1800s there was recognition of dramatic range deterioration in the United States as a result of overstocking of cattle (Bentley 1898). In his report, Bentley concluded that ''The ranges have been almost ruined, and if not renewed will soon be past all hope of permanent improvement.'' In spite of early recognition of a problem, solutions have still not been satisfactorily implemented (General Accounting Office 1992).

The impacts of grazing, whether positive or negative, may be extensive. In a recent biological assessment in the western Mojave Desert of California, 100% of a 234-square-km area was impacted to some extent by sheep grazing (Tierra Madre Consultants 1991). In a detailed analysis of the effects of sheep grazing on 2.6 square km of desert tortoise habitat, Nicholson and Humphreys (1981) observed soil disturbances in 80% of the area used by sheep. Thirty-three percent of the plot was heavily used by sheep.

Livestock grazing, by its very nature, causes a decrease in plant cover and biomass, at least initially. Decreases in cover have been shown to be associated with a decrease in the diversity and abundance of lizards and other wildlife species in arid ecosystems (Busack and Bury 1974, Germano and Hungerford 1981, Germano and others 1983, Germano and Lawhead 1986). In the Mojave Desert Nicholson and Humphreys (1981) observed large decreases in plant cover in areas grazed by sheep. Similar results were reported by Webb and Stielstra (1979) in the Mojave. In addition, they observed a 60% reduction in above-ground biomass on plots grazed by sheep. Other studies, in American deserts outside of the Mojave Desert, have not detected appreciable differences between grazed and ungrazed plots (Heske and Campbell 1991, Rice and Westoby 1978), but most sites had been grazed before the studies were initiated. An important point to make is that the response of plants to grazing varies according to species, season, plant phenology (Genin and Badan-Dangon 1991), local conditions (drought, edaphic factors, etc.), and past historical use.

Direct effects of grazing on desert animals such as the desert tortoise (*Gopherus agassizii*) are not well documented. Grazing sheep can damage tortoise burrows. Nicholson and Humphreys (1981) reported that of 164 tortoise burrows on a 2.6-square-km study site, 10% were damaged and 4% were destroyed. Most burrows were well protected since they were generally located under shrub cover. Damage was considered to be insignificant since tortoises were often observed digging new burrows in late spring regardless of the availability of existing burrows. Others have gone so far as to suggest that cattle dung actually serves as an important food supply for desert tortoises (Bostick 1990), although this has never been rigorously substantiated (Hal Avery personal communication).

Webb and Stielstra (1979) observed that soils in the Mojave Desert exhibited greater surface strength in areas where sheep bedded and grazed relative to control areas. The greatest compaction occurred in the upper 10 cm but compaction was also observed at lower depths. At the surface, soils are trampled by grazing, often obliterating cryptobiotic soil crusts leading to increased erosional potential. Erosion is of special concern for desert soils because the nutrient capital is often concentrated in the surface soil. Gross disorganization of community structure is possible with the loss of only a few centimeters of soil (Charley and Cowling 1968).

Even limited grazing can cause significant shifts in vegetation and damage to soil crusts. Kleiner and Harper (1977) found that seven plant species that were common in the ungrazed area were absent or insignificant in a comparable grazed section of Canyonlands National Park. They attributed this in part to changes in cryptobiotic soil crust, which decreased from 38% cover in the ungrazed area to 5% in the lightly grazed area. Grazing also increases the spatial and temporal heterogeneity of water, nitrogen, and other soil resources, fostering increased desertification of productive arid lands (Schlesinger and others 1990).

As stated above, the rate of natural recovery of habitats exposed to grazing depends on the intensity of past grazing and local conditions. In a blackbrush (*Coleogyne ramosissima*) association in Utah and Arizona, shrub cover is greater in areas that have never been grazed than in grazed areas. In the same area, plots protected from grazing for ten years showed no difference from heavily grazed areas indicating slow rates of recovery (Jeffries and Klopatek 1987). Exclusion of grazing for 14–19 years did not allow recovery of native perennial grasses in southeastern Arizona (Roundy and Jordan 1988). In the deserts of Kuwait land degradation does not necessarily stop following protection from grazing (Omar 1991). Drought, erosion, and sand encroachment continue to degrade land in the absence of grazing. Human activities and grazing may hasten degradation, but in concert with drought the three can be devastating.

In a recent review of the effects of grazing on public land in the hot deserts (Chihuahuan, Mojave, and Sonoran) of the American Southwest, the General Accounting Office (1992) concluded that a high environmental cost has been exacted on these fragile ecosystems and that land degradation due to grazing is continuing. The report concluded by noting that the high environmental risks, budgetary costs, low economic benefits, and management problems associated with livestock grazing on hot desert public lands merits Congressional consideration. Recommended options included raising grazing fees or appropriating additional funds to offset costs of administration and monitoring, and discontinuing livestock grazing altogether in hot desert areas.

Different plant communities respond to grazing in a variety of ways related to a complexity of factors. Results for the Mojave Desert suggest that livestock grazing can have locally significant effects on the plants (Figure 1) and ultimately on desert wildlife. Efforts to restore

Figure 1. Cattle grazing can have locally significant effects on vegetation and soils, as shown in this photo of a cattle watering area and corral in what is now the Mojave National Preserve, California. Note the almost total destruction of perennial plants in the immediate area. The visual effect is greatly diminished as distance from the watering area increases. Photo by Jeff Lovich.

degraded rangeland in the Mojave should start by considering the effects of grazing and the potential impacts of soil compaction, erosion, and plant community alteration.

Linear Corridors

Roads, railways, powerlines, and pipelines, some of the most conspicuous elements of the modern Mojave Desert landscape, are all characterized by long and relatively narrow corridors of disturbance. The fact that most linear corridors are narrow does not necessarily imply that their impacts are minimal. According to Brum and others (1983), over 8000 km of overhead power transmission lines were present in the California desert in 1980, impacting more than 28,000 ha of land. An additional 50,000 ha of land will be impacted by the year 2000 if the projected threefold increase in power demand is accurate. Information summarized in the California Desert Conservation Area Plan (Bureau of Land Management 1980) suggests that an additional 2000 km of energy production and utility corridors are needed to meet the needs of southern California to the year 2000.

The immediate effect of linear corridor construction on soil conditions and plant cover is one of nearly complete destruction (Vasek and others 1975a). In some cases recovery is retarded due to operation and maintenance of corridors (Artz 1989). Other negative secondary effects of corridors include mortality of animals along roadways (Rosen and Lowe 1994, Boarman and Sazaki 1996), habitat fragmentation and restriction of movements and gene flow, increased access to remote areas for illegal collection and vandalism of plants and animals (Nicholson 1978, Garland and Bradley 1984, Boarman and Sazaki 1996, Jennings 1991), and increased erosion (Wilshire and Prose 1987). The steel towers associated with many electrical energy transmission corridors provide nest sites and hunting perches for ravens (*Corvus corax*), a native predator that has increased dramatically in recent years due to human subsidy. The towers may allow ravens to hunt more effectively for the federally threatened desert tortoise (*Gopherus agassizii*) and other desert wildlife (Boarman 1993). Corridors can also serve as a source of exotic invasive plants brought in on construction equipment (Zink and others 1995). Invasive plants prosper in the disturbed conditions and contribute to an increased likelihood of fire. The construction of pipelines for gas, oil, and water and much more destructive than overhead lines because extensive trenching is usually required. This traditionally has led to severe soil impacts (leaving subsoil on the surface), disturbing stabilized crusts and rock surfaces, and concentrating runoff and erosion. More recent pipelines have incorporated some environmental protection and some rehabilitation but the low value of the desert land, the high cost of revegetation, and the lack of money for enforcement and supervision has often led to neglect and minimal treatment.

The impacts of linear structures can extend far beyond the boundaries of the immediate disturbance. Schlesinger and others (1989) studied the effects of diversion structures (earthen dikes) along the Colorado River Aqueduct on plants and soil. The structures were constructed to prevent runoff due to precipitation from washing sediments into open portions of the canal. Large areas downslope of the diversion structures received only incident precipitation, with essentially no runoff from the extensive drainages in the uplands above the diversion structures. As a result, large areas of desert habitat on the downslope side of the diversion structures had a lower biomass of perennial and annual plants in comparison to adjacent areas with no diversion structures.

Garland and Bradley (1984) observed that some species of rodents in the Mojave of Nevada are more abundant near highways, while others are not. However, reduced abundance may have been an artifact of natural habitat heterogeneity since no mortality was observed during the 11-month study. Another effect of roads is edge enhancement in which perennial shrubs along roadsides are denser, larger, more vigorous, and support greater numbers of foliage arthropods than those away from roadsides (Vasek and others 1975b, Lightfoot and Whitford 1991). Johnson and others (1975) noted that primary productivity, as measured by standing crop, at study sites in the Mojave Desert of California increased about 17 times on the basis of vegetated area alone and 6 times when the area of the bare road surface was included as part of the productive unit. Unpaved roads showed increases of 6 and 3 times, respectively, in each category. Increased water availability from pavement runoff and increased retention of moisture under the pavement are probably responsible for the observed increase in plant vigor, although removal of competing plants that formerly occupied the roadway may confer an advantage to plants along the berm (Vasek and others 1975a). The increase in vigor attracts herbivorous insects (Lightfoot and Whitford 1991).

The effects and recovery of linear corridor construction in deserts have been studied by several researchers. The process of natural recovery, following powerline construction in the Sonoran Desert starts immediately with invasion by pioneering annual species, but perennial species may not return for over five years. The density and diversity of annual species may increase in comparison with undisturbed sites, perhaps due to the removal of large woody species (Hessing and Johnson 1982). An effect that is apparently linked to changes in plant abundance and composition is a reduction in the density, but not the community composition, of arthropods following establishment of access roads for powerline construction (Johnson and others 1983).

In the Mojave Desert, plant cover also increases following powerline construction. The rate of increase and composition of colonizing species varies considerably, confounding the ability to predict succession relative to adjacent undisturbed areas. Ground cover of short-lived perennial species increases in areas of severe disturbance, under the central wires, and along the edge of maintenance roads. After 33 years there was a noticeable, but not complete, recovery of predisturbance vegetation (Vasek and others 1975b). Natural revegetation (0–41% ground cover) by long-lived perennials has been observed 12 years after construction of a pipeline by trenching, piling, and refilling (Vasek and others 1975a). Disturbed and control areas appear to have similar cover, biomass, and densities of vegetation following partial recovery, but similarities disappear when the proportions of long-lived and dominant species are compared (Lathrop and Archbold 1980a,b). Species with these characteristics are not well represented on disturbed sites.

Management strategies for minimizing the effects of linear corridor construction include: placement of power poles closer to existing access roads, modifying construction techniques for buried pipelines, less frequent road grading, and limiting the width of motorcycle race corridors along powerlines (Artz 1989). Lathrop and Archbold (1980b) proposed several recommendations for routing corridors to minimize environmental impacts including: (1) routing them through gently sloping areas to minimize erosion, (2) routing them through areas occupied by colonizing species such as cheesebush (*Hymenoclea salsola*), (3) avoiding areas dominated by high nitrogen fixation communities such as cat's claw acacia (*Acacia greggii*), and (4) avoidance of undue soil compaction with implementation of soil loosening efforts to aid natural revegetation. Revegetation of linear corridors was evaluated by Kay (1979, 1988), Graves and others (1978), and Brum and others (1983).

The slow recovery of the desert to linear corridor impacts is perhaps best demonstrated by the visibility of many of the old Native American trade routes. Long-term use by foot traffic alone was sufficient to compact the soil and recovery after several hundred years has not been enough to hide these trails (personal observation).

Mining

Mining has been an important activity in the California desert since the late 1880s. Mining communities such as Kokoweef, Hart Mountain, Boron, Johannesburg, and many others have had mostly localized impacts on the desert. The most obvious forms of degradation are pits, ore dumps, and tailings, but the once-great demand for fuel and timber, grazing, and road building associated with mines was unquestionably more important in the past. Fugitive dust and toxic tailings are a more recent concern from some of these mining areas.

The Bureau of Land Management (1980) estimated that 12,545 ha in the California Desert Conservation

Area had been affected by major mining operations. If the many small prospects and adits are included, the area affected by mining would certainly be larger. The brine evaporation and dry lake mine operations are extensive and lead to substantial wind erosion (Wilshire 1983). Another problem is animal mortality at poorly managed cyanide extraction gold mines in the Mojave Desert (Clark and Hothem 1991, Henny and others 1994).

Military Training Operations

Large areas of the California desert have been impacted by temporary and ongoing military activities. Major training exercises included activities by General Patton in the early 1940s, the Desert Strike operation in 1964, and Bold Eagle in 1976. Between 1942 and 1944 more than a million soldiers passed through these training facilities, which covered more than 46,800 square km (Bureau of Land Management, 1990). The camps were effectively small cities, up to 2800 ha in size (e.g., Camp Granite) (Prose and Metzger 1985). Continuing impacts are generated by active military bases including the National Training Center (at Fort Irwin, the Marine Corps Air Ground Combat Center at Twentynine Palms, China Lake Naval Air Weapons Station, and the Chocolate Mountain Aerial Gunnery Range (Lathrop 1983a). Military operations cause intensive damage in many areas but also provide protection of thousands of hectares from other sources of disturbance by prohibiting public access. At Fort Irwin alone, the area in need of remediation is estimated to exceed 50,000 ha.

The recovery of large areas of the eastern Mojave Desert subjected to military training exercises almost 36 years earlier was studied by Lathrop (1983b). Impacted areas included tent sites, roads, and tank tracks. All impacted areas exhibited significant reductions in plant density and cover relative to control areas. Reductions of cover and density were greatest in tank tracks and least in tent areas. Recovery to predisturbance levels of cover and density varied according to disturbance type. Tent areas showed the greatest recovery, and roadways showed the least, reflecting the intensity of disturbance. Recovery in tank tracks was intermediate. Diversity of dominant perennials also varied between disturbed and nondisturbed areas but results were clouded by low species richness at the study sites and small sample sizes of the subdominants. However, diversity in disturbed transects at the Camp Ibis study site was low relative to control sites. Species similarity decreased between control and disturbed transects with increased disturbance and use intensity.

Similar observations and conclusions were reached by Prose and Metzger (1985) and Prose and others (1987) at abandoned military camps in the eastern Mojave. Long-lived species such as *Larrea tridentata* were dominant in all control areas but percentage cover and density were reduced in impacted areas. Dominant plants in disturbed areas included pioneer species such as *Ambrosia dumosa* and *Hymenoclea salsola*. Percentage cover values for pioneer species in disturbed areas were equal to or greater than control values.

Differences in vegetative structure between control and impacted plots were due to soil compaction, changes in soil texture, removal of the top layer of soil, and alteration of drainage channel density (Prose and others 1987). Penetrometer measurements show that a single pass by a ‘‘medium’’ tank can increase average soil resistance values by 50% relative to adjacent untracked soil in the upper 20 cm, but values of up to 73% were recorded. Dirt roadways could not be penetrated with a penetrometer below 5–10 cm due to extreme compaction. Physical modifications to the soil beneath tank tracks extended vertically to a depth of 25 cm and outward from the track edge to 50 cm (Prose 1985).

Recovery times to predisturbance levels of density and cover were estimated by Lathrop (1983b) assuming linear rates (Table 1). Recovery to predisturbance species composition would require much longer, if it were to occur at all. Areas receiving the greatest amount of soil compaction, such as roadways, require the longest recovery times. Tank tracks and tent areas recover in a shorter amount of time. Overall, recovery in plant density is slow relative to increases in cover. In other words, the number of individuals changes little following recovery from disturbance, but surviving individuals cover larger areas. A major conclusion from Lathrop’s study was that recovery to some original level of community composition and stability may not occur in the foreseeable future. However, recovery of comparable disturbed areas has been excellent on restoration test plots at the Marine Corps Air Ground Combat Center near Twentynine Palms, California (Zink personal communication).

Off-Road Vehicles

Off-road vehicle (OHV) use is one of the major recreational activities in the deserts of California. The Motorcycle Industry Council estimated that 4.7 million motorcycles were used by 11.7 million people in 1978 for off-highway recreation in the United States, a figure that does not include dune buggies and four-wheel drive vehicles (Kockelman 1983).

The impacts of OHVs have been well documented (Webb and Wilshire 1983) and include destruction of soil stabilizers (see section on biotic components of soil), soil compaction, reduced rates of water infiltration, increased wind and water erosion, noise, decreased abundance of lizard populations (Busack and Bury 1974), and destruction of vegetation (Vollmer and others 1976). Compaction of a desert soil reduces the root growth of desert plants and makes it much harder for seedlings to survive (Bainbridge and Virginia 1990, Bainbridge and others 1995a). An excellent review of the effects of OHVs in the Mojave and other deserts is contained in Webb and Wilshire (1983) and the reader is referred to that document for information beyond that presented herein.

Soil compaction is a common effect of any compressive action on most soils. Compaction results from a variety of factors other than OHV use, including trampling by grazers, human trampling (Liddle 1991, 1997), and even raindrops (see review in Webb 1982). In the case of OHVs, compaction occurs at shallow depths related to the geometry of the contact surface between the tire and the soil interface. In one study the greatest increase in soil density occurred at a depth of 30–60 cm after being compacted by a motorcycle (Webb 1983). Soil density increases as a function of the number of vehicle passes, while soil infiltration rate decreases. Soils that are most susceptible to compaction are loamy sands and coarse gravelly soils with variable particle sizes. Wet soils are more susceptible to compaction than dry soil. Soils that are least affected include sands and clays.

Another by-product of heavy OHV use is increased wind and water erosion. The degree of erosion experienced in an area exposed to OHV use is affected by two main factors. First, increased water erosion is partially attributable to decreased infiltration rates due to compaction. Second, OHVs destroy surface stabilizers (see section on biotic components of soil), making soils more susceptible to erosion (Hinkley and others 1983). The enormity of the problem in the Mojave Desert is underscored by the fact that satellite photos revealed six dust plumes covering over 1700 square km of the western Mojave on 1 January 1973 that were attributed to surface destabilization primarily by OHVs (Nakata and others 1976, Gill 1996).

As shown in numerous photographs in Webb and Wilshire (1983), the effects of erosion can have indirect effects, since debris flows (Nakata 1983) can bury plants at some distance from the impacted area. Areas that are least susceptible to water and wind erosion following OHV use are dunes, playas, and areas with abundant coarse surface material (Gillette and Adams 1983, Hinckley and others 1983). Restoration of OHV areas affected by erosion requires actions to not only stop continuing erosion (Harding 1990, Heede 1983, Middleton 1990), but also action to restore past damage.

Desert soils vary in their susceptibility to OHV damage. Susceptibility is generally high in all areas except barren sand dunes (but see Bury and Luckenbach 1983), and the clay flats of playas. Soil damage caused by OHVs is environmentally significant due to the fact that desert soils may take 10,000 years to develop (Dregne 1983). From this estimate, Dregne concluded that it was futile to speak of disturbed soil recovery in time frames related to human occupancy.

Another major effect of OHV use is the destruction of plants. Lathrop (1983a) examined aerial photographs of nine disturbed and undisturbed areas in the Mojave Desert to assess the effects of OHV usage. Perennial plant density and cover were dramatically reduced in OHV areas. The percentage of cover and / or density in OHV-impacted areas relative to control areas was less than 15% in three of the sites examined. Destruction of plants resulted not only from crushing stems and foliage, the extensive root systems that fill the intershrub spaces, and germinating seeds, but also from the superstructure of the vehicle. The latter factor is important since it is responsible for plant destruction in an area wider than the track width of the vehicle. The wheel tracks of a full-size off-road vehicle operating in an undisturbed area can damage almost 0.5 ha of land with every 6.44 km traveled. Support vehicles, including very large and heavy motor homes, are very destructive, and camping areas are especially hard hit.

An easily detected but poorly understood effect of OHVs is noise. Noise from certain types of OHVs can reach 110 decibels, which is near the threshold of human pain. Brattstrom and Bondello (1983) demonstrated that OHV use in the Mojave Desert caused noise levels that caused hearing loss in animals such as kangaroo rats, desert iguanas, and fringe-toed lizards; interfered with the ability of kangaroo rats to detect predators such as rattlesnakes; and caused unnatural emergence of spadefoot toads that were estivating until the arrival of rain for breeding, a situation that could result in death. The authors noted that although OHVs are not the loudest source of human-generated sound in the Mojave, they occur more frequently than any other high-intensity sound source. In their report, Brattstrom and Bondello recommended that OHV areas be located away from the ranges of ‘‘all undisturbed desert habitats, critical habitats, and all ranges of threatened, endangered, or otherwise protected desert species.’’

The impact of OHV use on desert tortoises in the Mojave Desert of California was examined by Bury and Luckenbach (1986) in an unpublished report. Significantly more tortoises and active burrows were found on a 25-ha control plot than on a similar plot exposed to OHV use. In addition, subadult and adult tortoises on the control plot exhibited larger body mass than those on the OHV plot.

Impacts related to OHV use present a serious challenge to desert restoration projects for three reasons: (1) the potentially severe impact of OHV use in desert ecosystems, (2) the widespread nature of the OHV impacts in the California desert, and (3) the fact that OHV areas are often located in or near environmentally sensitive habitats. Areas targeted for restoration should be closed to OHV use prior to initiating procedures to ameliorate past damages.

Invasive Plants

Invasive exotic plants have had a significant impact on the natural communities of California (Mooney and others 1986, Rejmánek and Randall 1994), including the southern California desert ecosystem. Invasion has been facilitated by habitat disturbances that allow exotic species to colonize habitats once dominated by native species (Hunter and others 1987). Once established, exotic plants may diminish the abundance of native species due to competitive interactions or by disruption of natural processes such as fire frequency and intensity.

Some of the more important exotic plants in the southern California desert are saltcedar (*Tamarix ramosissima*), also known as tamarisk (Lovich and de Gouvenain 1998), Russian thistle (*Salsola iberica*) (Young 1991), filaree (*Erodium cicutarium*), and several grass species including split grass (*Schismus* spp.) and bromes (*Bromus* spp.) (Brown and Minnich 1986, Hunter 1991). Immense areas of desert are colonized by these species. Although other exotic plants are present in the Mojave Desert, these are important because of their ubiquity.

Exotic plants present two major problems to the integrity of the desert ecosystem. First exotic annuals increase the fuel load and frequency of fire in a community that is poorly adapted to fire. Second, some exotic plants exhibit allelopathic effects that negatively affect native species, especially annuals. Negative interactions have been demonstrated between Russian thistle and other species in the laboratory (Allen 1982a, Lodhi 1979). In addition, competition of Russian thistle with native perennial grasses increases under drought conditions (Allen 1982b), furthering establishment of the exotic. Fortunately, Russian thistle competes poorly with established vegetation and rarely supplants well-established native populations. Unfortunately, once the soil is disturbed and native plants are eliminated, Russian thistle gains a strong foothold (Young 1991). General reviews of the threats posed by exotic species invasions in native ecosystems are summarized by Cheater (1992) and D'Antonio and Dudley (1993).

Air Pollution

One of southern California's most famous exports is smog. While most noticeable in the inland valleys of the state, smog is often transported via atmospheric processes into the Mojave Desert (Pryor and Hoffer 1991). Anthropogenic pollutants include ozone, sulfur dioxide, and various particulates. Atmospheric tracer experiments have shown that pollutants released in the San Fernando Valley impact the southern Mojave Desert towns of Adelanto and Palmdale, while those released in the southern San Joaquin Valley impact the northern Mojave Desert towns of Mojave and China Lake (Reible and others 1982). Experimental tracers used in atmospheric transport studies are diluted by factors of only 2–3 during passage between source and receptor areas. Impacts are maximized during evening and nighttime hours, independent of the time of release in the San Joaquin Valley, because of the diurnal mountain–valley wind cycle. Ozone levels in the Mojave Desert can exceed 100 parts per billion (ppb) or more when offshore wind transports atmospheric pollutants from the Los Angeles Basin (Thompson and others 1984a). By comparison, ozone levels in remote areas range from 20 to 40 ppb.

The most obvious effect of smog in the Mojave Desert has been visibility degradation in an area historically distinguished by extraordinary visibility (Walsh and Hoffer 1991). Median visibility is 48–88 km in large urban areas and 104–128 km in nonurban locations. Visibility has decreased 10%–30% from the middle of the 1950s to the early 1970s at many recording stations (Trijonis 1979).

Much of the visibility loss is related to particulates, including nitrogen-rich compounds. Dryfall of these compounds from air pollution can be a major source of supplemental N for plants. This favors many exotic plant species over native annuals and perennials. Wedin and Tilman (1996) found that half the native plant species in a Minnesota grassland were lost from the community at supplemental N levels mimicking dryfall deposition rates.

A less obvious effect is damage to plants. Stolte (1991) observed injurious effects to desert plants exposed to ozone and sulfur dioxide in laboratory experiments. Annual plant species of the genera *Camissonia* and *Cryptantha* exhibit high sensitivity to both gases. The grass *Oryzopsis hymenoides* exhibits high sensitivity to sulfur dioxide, as do some types of cryptogamic soils. Responses of cryptogamic soils include increased electrolyte leakage, chlorophyll degradation, and reduced nitrogen fixation (Belnap 1991).

Studies of plants from the Mojave and Colorado Deserts show that perennial species vary in their re-

Figure 2. The effects of fire in the desert are obvious in this photo taken near Palm Springs, California, about five years after the blaze. Note the almost complete elimination of perennial shrubs in the burned area to the left. Perennial plant species in the Mojave and Colorado Deserts are long-lived and very sensitive to fire, traits that collectively contribute to the long recovery times typical of many desert plant communities after fire. Photo by Jeff Lovich.

sponse to SO_2 and NO_2. *Larrea tridentata* is sensitive to fumigation by these pollutants under experimental conditions, displaying extensive leaf injury and reduced growth or dry weight. *Encelia farinosa* and *Ambrosia dumosa* show intermediate responses, while *Atriplex canescens* appears to be resistant (Thompson and others 1980). Sensitivity also varies among native annual plants, with *Camisonia claviformis*, *C. hirtella*, and *Cryptantha nevadensis* exhibiting leaf injury at low concentrations of SO_2 and O_3 (Thompson and others 1984b).

Fisher (1978) suggested that high rates of mortality in desert holly (*Atriplex hymenelytra*) in the northern Mojave Desert (Death Valley) were related to elevated ozone levels. During the summer months he recorded ozone levels that were twice the national standard of 0.08 ppm. Photosynthesis and water use was significantly reduced in greenhouse experiments where seedlings were exposed to 0.15–0.18 ppm ozone for 3 h. Ozone-induced reduction in water-use efficiency was postulated to be the cause of declining *Atriplex* populations in Death Valley.

Additional summaries of the impacts of air pollution in the Mojave and Colorado Deserts are provided by Mangis and others (1991), Thompson (1995), and VanCuren (1995).

Anthropogenic Fire

Fire was not an important factor in shaping the prehistoric structure and dynamics of plant communities in the California desert. The infrequency of fire in the prehuman landscape of the desert was due to limited biomass, large intershrub spacing, low combustibility of some native plants, sparse groundcover to support and propagate combustion, and the absence of human-mediated fire suppression activities (Humphrey 1974, O'Leary and Minnich 1981, Minnich 1983, Brown and Minnich 1986). Such is not the case in other desert and semidesert areas of the American Southwest, including parts of the Sonoran and Chihuahuan deserts, where fire was an important prehistoric agent in maintaining grassland seral stages (Humphrey 1958, 1963, 1987, Reynolds and Bohning 1956).

The proliferation of exotic annual plant species such as *Bromus*, *Schismus*, and *Salsola* has dramatically increased the fuel load and frequency of fires in many ecosystems around the world (D'Antonio and Vitousek 1992), including parts of the California desert (O'Leary and Minnich 1981, Brown and Minnich 1986), in recent years. The frequency of fires in the Colorado Desert of California is further enhanced by the proximity of previously burned areas (Chou and others 1990). Native perennial shrubs are poorly adapted to relatively low-intensity fires as evidenced by low rates of recovery (Figure 2). In the upper Coachella Valley on the east scarp of the San Jacinto Mountains near Palm Springs, California, burned creosote bush scrub is replaced by open stands of *Encelia farinosa*, native ephemerals, and exotic species such as *Schismus* and *Bromus* (Brown and Minnich 1986).

Postfire vegetational recovery along a chaparral–desert ecotone including parts of Anza-Borrego Desert State Park in San Diego County, California was examined by Tratz and Vogl (1977). They observed high recovery (as measured by speed of resprouting) in chaparral shrubs and desert-wash plants, but low recovery in cacti. Herbivorous mammals present before the burn were also present afterwards, since rapid recovery of shrubs provided adequate food supplies for wildlife, even in the first months after the fire. If California desert perennial plant communities are not well adapted to fires, animals that coevolved in the ecosystem should not be expected to respond favorably to fire either.

According to fire personnel at the California Desert District (CDD) Office of the Bureau of Land Management (BLM), the CDD (including the Mojave and Colorado Deserts) had a ten-year average of 175 fires per year prior to 1992 (range 100–475) that affect an average of 10,927 ha annually (range 607–34,400 ha). The CDD estimates include a very small amount of BLM land outside the desert.

Impacts on Biotic Components of Soil: The Invisible Component of Biodiversity

Although emphasis is often placed on the physical and chemical properties of various soils, they contain important biotic components as well including: soil surface stabilizers such as algae and lichens, nematodes and other metazoans, various bacteria, and mycorrhizae. Odum (1994) referred to these organisms as the invisible component of biodiversity. While not as conspicuous as macrofloral elements, biotic components of soil are important symbionts that are easily destroyed by certain human activities.

Undisturbed desert areas are characterized by the presence of soil stabilizers, including lichen, fungal, bacterial, and algal crusts; desert pavement; mechanical crusts; and chemical crusts. The biotic components of these stabilizers are collectively referred to as cryptobiotic soil. Mineral-derived crusts form under a variety of physical and chemical conditions that may actually be facilitated by biotic components (Elvidge and Iverson 1983, Taylor-George and others 1983). Soil stabilizers are important agents in preventing erosion but are easily disturbed since they occur at the surface. Stabilization mechanisms include binding soil particles with thallial filaments in the case of biotic stabilizers, armoring the surface, and increasing surface roughness. Crusts also provide germination sites for vascular plants (but see Wood and others 1982), and conserve water (see review in Cole 1990). The susceptibility of crusts to damage varies according to the composition of the underlying soil. In soils subjected to large shear stresses, a single pass by a vehicle is capable of destroying well-developed crust. When the forces are mainly compressive, crusts can survive a single pass in a slightly modified form; however, OHV use is capable of quickly eliminating crusts in an impact area (Wilshire 1983).

Considerable research has been conducted on the impacts of grazing and other agents of trampling on cryptobiotic soil crusts. These crusts are very important not only because of the soil-stabilization functions mentioned above, but because they facilitate the accumulation of organic material and soil nutrients, particularly nitrogen in the upper layers of soil (Kleiner and Harper 1977, Johansen 1993), and enhance soil moisture retention (Belnap and Gardner 1993). Research in desert and semidesert areas in Utah and Arizona has consistently shown that cryptobiotic soil is heavily impacted by grazing, even light winter grazing (Kleiner and Harper 1977, Anderson and others 1982, Brotherson and others 1983). Impacts include the destruction of surface pinnacles associated with development of cryptogamic soils (Anderson and others 1982) and the virtual obliteration of biotic elements (Cole 1990). Lichens and mosses are most sensitive to disturbance, with algal components being more resilient (Brotherson and others 1983).

Cole (1990) conducted an interesting experiment at Grand Canyon National Park to examine the effect of trampling by hikers wearing lug-soled boots. Only 15 passes were required to destroy crusts. Visual evidence of biotic components was reduced to near zero after 50 passes. The results of Cole's experiment clearly illustrate the fragility of crusts to trampling.

Cryptobiotic soil recovery may require long time intervals without intervention. Following exclusion of grazing in a Utah semidesert study site, cryptobiotic cover increased from 4%–15% in 14–18 years, but only 1% per year for the next 20 years (Anderson and others 1982). Cole (1990) observed partial recovery from human trampling in one to three years and extensive recovery after five years. However, surface irregularities associated with well-developed cryptogamic cover remained low even after five years, suggesting that recovery was incomplete. Belnap (1993) noted that over 250 years may be required for full recovery on the Colorado Plateau. Recovery was improved but was still very slow when scalped experimental plots were inoculated with crusts from surrounding areas. In the northern Mojave Desert, lichen crusts may not reoccupy heavily disturbed areas even after 63 years (Wilshire 1983). Details of the formation and recovery of chemical and mechanical crusts are discussed in detail by Wilshire (1983). The nitrogen-fixation capabilities of damaged soil may take over 50 years to recover (Belnap 1995).

Important symbiotic relationships have developed between certain species of vascular plants and vesicular–arbuscular mycorrhizal (VAM) fungi and rhizobia. The small-diameter hyphae of symbiotic fungi serve as energy efficient root hairs, enabling the host plant to better absorb nutrients, particularly phosphorus (Bloss 1985) and water (Bethlenfalvay and others 1984). Rhizobia are bacteria capable of fixing atmospheric nitrogen for use by plants. The importance of VAM fungi in desert plant communities is underscored by the fact that in a recent survey of 38 plant species (19 families) in Anza-Borrego Desert State Park in the Colorado Desert of California all were colonized by VAM species (Bethlenfalvay and others 1984). Plants naturally associated with VAM that are also found in the western Mojave Desert include *Hymenoclea*, *Ambrosia*, *Opuntia*, and *Larrea*. Bloss (1985) reported numerous plant associations in the Sonoran Desert of Arizona as well.

Previous studies have demonstrated the importance of maintaining and enhancing soil microbes in restoration projects (St. John 1984, Bainbridge 1990). Establishing plants in disturbed areas with marginal soils may be difficult or impossible without the presence of a vigorous population of microbial symbionts. These symbionts are adversely affected by soil compaction. Studies have shown 1–2 m of hyphae per gram of soil in Mojave and Sonoran soils, yet virtually none in disturbed areas (Zink personal communication). Restoration is complicated by the fact that fertilizers can inhibit mycorrhizae growth.

Can the Desert Be Restored?

Plant growth and establishment are naturally slow under the extreme conditions of the desert, and disturbance makes these conditions even more severe (Bainbridge 1990). Disturbance typically reduces both the infiltration of water into the soil and the moisture-holding capacity of the soil (Bainbridge and Virginia 1990). This increases the value of rapid deep root growth, which is made more difficult by increases in soil strength from compaction and reduced soil moisture. These synergistic effects make plant establishment much more difficult after disturbance. Revegetation and restoration work can help mitigate many of these impacts and speed recovery, but the severe conditions and unpredictable rainfall still make restoration of these sites very challenging.

A brief history of revegetation studies in the deserts of California was provided by Kay and Graves (1983). Studies in the Mojave Desert are few and relatively recent. One of the earliest studies evaluated the success of revegetation efforts along the second Los Angeles Aqueduct (Kay 1979, 1988). Construction involved stripping the vegetation from an area 200 km long × 60 m between 1968 and 1970. The seeds of seven species of native plants were distributed at six 2- to 15-ha sites on the aqueduct. The seeds of all but one species, *Atriplex polycarpa*, were from local stock. Surface preparation involved ripping the soil to 25 cm on 60-cm centers to relieve compaction. A rangeland drill was used to set the seeds at a depth of about 1 cm. Success varied among plant species. *Ambrosia dumosa* exhibited good establishment on three of six sites, but only one site had numbers approaching that of adjacent undisturbed areas. *Larrea tridentata* exhibited similar results. The other species, including *Atriplex polycarpa*, *Ephedra nevadensis*, *Hymenoclea salsola*, and *Lepidospartum squamatum*, were totally unsuccessful. *Atriplex canescens* suffered as a result of heavy grazing. The most abundant shrub along the aqueduct, *Chrysothamnus nauseosus*, established itself naturally, although it was uncommon in adjacent undisturbed areas. Kay (1988) concluded that natural revegetation is good in many years and poor in others, while artificial seeding did not consistently hasten or improve plant recovery.

In another experiment along the aqueduct, Graves and others (1978) tested the effects of a single irrigation and the success of direct seeding versus transplanting. The two methods of establishment exhibited widely variable success rates from site to site and according to species, but were not enhanced by irrigation. Substrate characteristics may influence the success of irrigation as measured by the appearance of native winter annuals (Johnson and others 1978).

The overall success of the revegetation attempt along the aqueduct was low. The vast majority of the aqueduct was still a highly visible scar in the early 1980s (Kay and Graves 1983), but recovery was inhibited by grazing and OHV use. Conclusions from the study were that more attention should be focused on establishment of visually dominant species such as *Larrea tridentata*, seeding should take place as soon after disturbance as possible, areas should be protected from grazing and OHV use, and local seed stock should be utilized for all species.

Highway revegetation studies were also reviewed by Kay and Graves (1983). Survival of container-grown shrubs planted in October 1973 and February 1974 at a site in Mojave, California, was 90% in May 1974. The roots of the transplants were exposed after a heavy rain in December 1974, and all plants were dead by October 1975. *Atriplex* spp., *Chrysothamnus* spp., and *Ephedra* spp. exhibited the greatest survival. Success was limited by rabbit overgrazing and competition from Russian thistle (*Salsola*). Container plantings were more successful when planted in the late winter or early spring. Application of fertilizer encouraged both the invasion of native woody shrubs and the nonnative annual grass *Schismus arabicus*.

Others have experienced similar success in revegetation. Brum and others (1983) observed low, long-term seedling establishment for a variety of species under several irrigation treatments along a powerline transmission corridor. The overall germination–establishment rate for seedling and postseeding irrigation success was 0.3%, and 26% for transplanted seedlings. *Larrea* exhibited poor germination under field conditions and responded poorly to all revegetation attempts.

More successful revegetation has been achieved at the Nevada Test Site in the northern Mojave Desert (Romney and others 1990). Greater than 80% survival of transplanted native shrubs and grasses was achieved when plants were protected from jackrabbits and irrigation was provided periodically.

Restoration efforts in the Colorado Desert of California were reviewed by Bainbridge and Virginia (1990). Although the plant communities differ somewhat between the Colorado and Mojave Deserts, both ecosystems pose similar challenges to restoration attempts: high temperatures, intense sunlight, limited moisture availability, high levels of herbivory by rodents and rabbits, and low soil fertility. Much of the success in revegetation experiments in the Colorado Desert is due to efforts to protect plants from herbivores and the use of buried water reservoirs for irrigation. Direct seeding attempts have generally been unsuccessful relative to transplants. *Larrea tridentata,* in particular, responded well to transplanting, especially if pruned prior to planting to increase the root-to-shoot ratio.

Assessing the nature and magnitude of human-induced disturbances makes restoration planning more efficient by enabling limited resources to be directed at critical problems. Ongoing studies (Bainbridge and others 1995a,b) of the effectiveness of desert restoration techniques are steadily advancing our ability to rehabilitate degraded arid lands in the southwestern United States, and the reader is referred to these references for details beyond the brief overview given in this section.

Plant recovery usually requires container-planting activities as well as site improvement. The most common method of direct seeding is simple hand seeding, which allows species to be matched to specific site conditions, appropriate planting depths, and results in a more natural appearance than machine planting. However, limited rainfall and removal of seeds by rodents and harvester ants may severely limit seedling establishment during typical years.

Transplanting is increasingly being used to provide nurse and seed plants for the disturbed areas (Bainbridge and others 1995b). The dominant shrubs and trees of the Colorado Desert are relatively easy to grow in a nursery or maintained landscape setting, and they are well adapted to transplanting with after-care. They are more challenging to establish in the field in a low- or no-maintenance situation, although once established, growth rates can be high. Reestablishment of annuals has been more difficult. New containers and soil mixes have improved plant survival. Deep pipe and buried pot irrigation and hand watering have also been effective. Tree shelters to limit herbivory and wind damage are also important.

A full appreciation of the ecological setting and adaptation of desert plants can make establishment less costly and more successful, but it is still expensive. The cost of restoring road edge areas in Joshua Tree National Park is fairly well established (after almost 10 years of work) and runs up to $15,000 per ha to establish large potted perennials in areas that are easily accessed. The cost of duplicating this type of work at remote sites would be much higher. Research conducted by colleagues at San Diego State University has emphasized lower-cost, less-intensive restoration, but the costs (excluding research) are still on the order of $12,000–25,000/ha. Even these high project costs provide no guarantee of success.

Conclusions

Desert areas disturbed by human activities may take centuries to recover without active intervention. Undisturbed desert soils are often in a relatively stable equilibrium developed over hundreds or thousands of years. Removal of vegetation and disturbance of soil crusts or soil structure can destroy this equilibrium, leading to wind and water erosion that are very difficult or impossible to control without very high investments in material and labor.

One of the key lessons of our research in the Mojave and Sonoran deserts is the critical importance of minimizing the intensity, frequency, and area of disturbance. Past research summarized in this paper has identified the wide range of effects from human disturbance and the difficulty and the high cost of mitigating damage. While recovery rates can be increased with modest expenditures, a major restoration program to improve recovery for just the OHV-damaged areas in the California desert region could exceed one billion dollars. Available funding will permit only a limited restoration for selected sites, even with continuing generous contributions of volunteer labor. Fences, signs, and enforcement to prevent further damage may often be a better investment than intensive restoration.

Recent research in the Mojave Desert demonstrates the benefits that protection can impart, even to previously disturbed areas. Brooks (1995) conducted a comparison between the Desert Tortoise Research Natural Area (DTNA) and unprotected land immediately adjacent. The DTNA was fenced to prohibit both OHV use and sheep grazing between 1978 and 1979. By the time of his study in 1990–1992, Brooks demonstrated that aboveground live annual biomass was generally greater inside than outside the fenced area, with the exception that the exotic annual grass *Schismus barbatus* produced more biomass outside the fenced area. Percent cover of perennial shrubs, seed biomass, and rodent density and diversity were also greater inside the fenced area.

To be successful, revegetation and restoration require careful attention to ecological relationships, both above and below ground, herbivory, soil characteristics, microclimate, and patterns of moisture availability (Bainbridge 1990, Bainbridge and others 1995a). Undoing the damage done to the soil system by disturbance is a critical step toward recovery and restoration. In general, strategies that recreate or mimic natural conditions are most likely to speed recovery of the entire ecosystem.

Research conducted in the Mojave and Colorado desert ecosystem has important applications for the American Southwest and throughout the world's arid zones. These areas have deteriorated rapidly under pressure from overgrazing, poor farming, and removal of trees and shrubs for fuelwood. The lessons learned in the desert ecosystem of southern California may help people living in these areas to protect or restore the productivity of their lands, and improve their lives.

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THE EFFECTS OF WILDFIRE ON REPTILE POPULATIONS
IN THE MOJAVE NATIONAL PRESERVE, CALIFORNIA

Final Report
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ABSTRACT

During the summer of 2005, lightning caused wildfires in the Mojave National Preserve, California. The fires burned 287 km^2 and left unburned patches surrounded by burned vegetation.

This study examined the effects of the wildfires on reptile diversity and *Uta stansburiana* (side-blotched lizard) abundance by conducting transect surveys at patches and along the fire perimeter in burned and unburned habitats. Temperature and vegetation cover data were recorded at each site. Pitfall trapping was conducted at patch sites to monitor *U. stansburiana* movements.

The wildfires resulted in higher temperatures in burned areas and more cover in unburned areas. Burned and unburned habitats had comparable reptile diversity and *U. stansburiana* was most abundant. *U. stansburiana* in unburned perimeter locations were constant, indicating this population was the least impacted. In 2006 the most were found along the burned side of the perimeter where high temperatures may have allowed for optimal basking sites. In 2007 the temperatures increased and the individuals in this area decreased by half.

The number of individuals moving out of patches was consistent but the number moving in increased, indicating a preference for unburned areas. The low numbers recorded in this study suggest that the wildfire negatively impacted the herpetological community.

INTRODUCTION

Ecological Role of Wildfire

Disturbance is common to all ecosystems and results in altered landscapes that differ from original habitat in floral and faunal composition and abundance (Reice, 2001). Natural disturbance, particularly wildfire, causes habitat changes by killing mature plants, seedlings, and seeds. Fire also alters the nutrient levels and water absorption abilities of soil. The effects of fire result in changes in microclimate, particularly post-fire soil temperature and moisture, and drastically reduce ground cover (Brooks, 2002; Odion and Davies, 2000).

In systems that are fire adapted this disturbance is essential for floral and faunal persistence (Parr and Chown, 2003). However, in areas that have not historically been subjected to frequent or intensive fire regimes, such as arid ecosystems, species diversity and abundance suffer due to mortality during the fire and the subsequent alteration of habitat (Brooks and Matchett, 2003; Taylor and Fox, 2001).

The unpredictable nature of wildfires often creates a habitat framework of small unburned patches within what was once contiguous habitat (Parr and Chown, 2003; Turner et al., 1997). Wildfire thus fragments habitat by creating small patches that are separated from one another by a habitat type that no longer resembles original conditions. Fragmentation due to wildfire does not necessarily indicate permanent habitat loss (Fahrig, 2003). The effects of wildfire are unpredictable and recovery is highly variable depending on location, burn severity, intensity, and post-fire plant succession (Davies et al., 2001; McKenzie et al., 2004; Reice, 2001; Turner et al., 1997).

Fragmentation, Wildfire, and Reptile Communities

A review of herpetofaunal response to fire found that many animals exhibit panic and experience high rates of mortality (Russell et al., 1999). Because of the need for thermoregulatory, foraging, and protected sites, reptiles are highly dependent on habitat structure and fire has been shown to reduce their abundance and limit movements (Setser and Cavitt, 2003; Valentine et al., 2007). However, unburned habitat patches may serve as refugia for reptile populations that survive in the patch, nearby rock outcroppings, or burrows in the ground (Faria et al., 2004; Friend, 1993).

While vegetated areas produce shaded microclimates where soil temperatures are less extreme and moisture is preserved, disturbed habitats generally show reduced vegetation complexity (Patten and Smith, 1975). Habitats dominated by invasive plants also show decreased numbers of invertebrates. This reduction in thermoregulatory and food resources results in a decrease in total reptile abundance. Studies in disturbed areas in southern California, Australia, and Egypt have indicated that reptile abundance and diversity were positively correlated with vegetation percent cover and native vegetation (Attum et al., 2006; Russell et al., 1999; Valentine et al., 2007).

Wildfire and Exotic Plants in Desert Regions

Historically, large wildfires in desert communities have been uncommon because without a relatively large, continuous fuel source, wildfires tend to have reduced size and intensity (Hanes, 1971; Reice, 2001). However, in North American deserts, wildfires have become increasingly frequent since the 1970s. This is because of the introduction of exotic plant species, particularly *Erodium cicutarium* (fillaree), *Bromus sp.* (foxtail, cheatgrass) and *Schismus sp.* (Mediterranean grass). These species, native to Europe, Africa, and Asia, are adapted to fire regimes in arid ecosystems and create a blanket of dry vegetation that facilitates the spread of wildfire by creating a layer of dry, fast burning fuel. Recurrent fire in the American southwest amplifies the presence of these alien species, which have been shown to replace long-lived natives, changing the floral composition (Brooks, 1999, 2000a, 2000b; Brooks and Matchett, 2003; Esque, 1999; Young, 2000). Because of these effects wildfire is currently considered one of the main threats to native species in the Mojave (Brooks, 2002).

Wildfire in the Mojave Desert

The Mojave Desert is subjected to frequent lightning strikes during the summer monsoon season (May-August) and wildfires are generally caused by dry lightning storms during this period (Esque et al., 2003). Large fires are infrequent events in areas with native vegetation. Consequently, wildfires in the Mojave have not been well studied, and their effects have yet to be well documented (National Park Service, 2003).

On 22 June 2005, a series of dry seasonal storms passed through the Mojave National Preserve (MNP), San Bernardino County, California. Dry lightning caused multiple fires that merged to become the Hackberry complex of wildfires. The fires burned for seven days and were contained on 28 June 2005. A total of 287 km^2 burned within the Preserve between elevations of 1097-2012 m (http://www.nps.gov/moja/parkmgmt/upload/Hackberry_BAER_Plan%2006-05.pdf). Within the Hackberry region the dominant form of vegetation affected by the fires was juniper woodland (Mojave National Preserve Maps, 2005). However, the fire did not consume all of the vegetation and the burned landscape contained several patches of unburned habitat. These habitat islands were surrounded on all sides by burned vegetation resulting in a fragmentation of the habitat.

Objectives

The Mojave is home to an incredible array of reptiles and the Hackberry region supported many species. The objective of this study was to determine the effects of the Hackberry wildfires on the herpetofaunal community. Based on previous research, most of which indicates increased mortality as well as limited habitat utilization and movement following a wildfire, it was reasonable to expect populations in the Mojave would show similar responses. I expected to find increased ground and subterranean temperatures and decreased vegetation cover in burned areas, with cover increasing through time, but not achieving pre-burn proportions or composition. The burned locations were expected to support fewer reptile species based on the resources available. As density increased with time, more individuals were expected to disperse from unburned habitat patch locations. I tested the hypothesis that movement into and out of unburned habitat patches by would change with time. I predicted that in the first year of this study more individuals would migrate into unburned habitat patches and that in the second year the individuals would disperse out of patches as lizard density and vegetation in burned areas increased.

MATERIALS AND METHODS

Site Selection

The Mojave National Preserve (MNP) lies in the eastern portion of the Mojave Desert of California. The Preserve is located to the south of Death Valley and north of Joshua Tree National Parks, between Interstates 15 and 40. The infrequency of large wildfires, remoteness of the area, and limited impact from development make the MNP an excellent area to study. Permits were obtained from the National Park Service, California Department of Fish and Game, and California State University (IACUC number 279).

Sampling for this study was concentrated in what was predominantly juniper woodland between the elevations of 1,370 m-1,675 m (Mojave National Preserve Maps, 2005). Sites were located near Cedar Canyon and Black Canyon roads, in the Mid-Hills area (Figure 1). Seven unburned habitat patches, that were surrounded by burned landscape on all sides, and seven perimeter locations along the fire edge were surveyed. Patch sites were mapped using a handheld Global Positioning System (GPS) unit and ranged in size from approximately 1,527-36,580 m^2.

Temperature Data Collection

Ambient, ground, and subterranean temperatures were collected using a handheld Ashcroft dial thermometer. All temperatures were recorded after the thermometer was placed in a temporarily shaded area for 2 minutes and collected at the start of each transect survey on both the burned and unburned sides. Air temperature was recorded after holding the thermometer several feet above the ground, ground temperature was recorded after placing the thermometer on the soil surface, and subterranean temperature was recorded after placing the tip of the thermometer 3-5 cm into the soil.

At one habitat patch an Eastman maximum/minimum thermometer was installed on a wooden stake 50 cm above the ground to determine air temperature extremes.

Transect Design

Transects were used to assess species diversity and abundance across distinct habitat types with clearly defined borders (Morris, 1995). At each sampling site three parallel transects that crossed the transition zone from burned into unburned habitat were monitored. Each transect was a straight-line 50 m in length, and bisected the habitat, with 25 m in each habitat type. Transects were separated from replicates by 20 m (Figure 2). Transects were measured out using a 25 m Lufkin tape measure. I used GPS waypoints to mark the start and end locations of each transect (Table 1).

Vegetation Point-Intercept Transect Surveys

Vegetation point-intercept transects were conducted by walking the transect lines described above and recording vegetation height every five meters. At each point a 7-cm diameter pole was placed directly on the point and the height of each plant that touched recorded (Barbour et al., 1999). Plant height was classified as <10 cm, 10-30 cm, 30-50 cm, 50 cm-1 m, and >1 m. Dead or severely burned vegetation was not recorded. I recorded vegetation once a month from May-October 2006 and March-August 2007. A total of 504 vegetation transects were conducted (14 sites x 3 replicates x 12 times).

Reptile Transect Surveys

During the fall and spring, transect surveys were conducted throughout the day; however, in the summer, when temperatures were at their highest, transect surveys were conducted in the morning and late afternoon. In order to find lizards by direct observation in both burned and unburned areas, each transect line was walked two times and a snake stick used to flush lizards from grasses and shrubs. Sighting effort was concentrated to 5 m on either side of the transect line. Reptile species were identified, and distance along the transect line was documented in 5 m segments. During the course of this study I conducted a total of 1,542 transects (14 sites x 3 replicates x 36 times).

Pitfall Trapping

Pitfall arrays were established at the seven habitat patches to determine the diversity of reptile species in patches and monitor movements (Table 2). At each patch six 5-gallon plastic buckets were buried so the rims were flush with the soil surface. Three drainage holes were drilled into the bottom of all traps to prevent the accumulation of water. Each trap was fitted with a cover to provide shade and protection. The covers were inverted plastic bucket lids with three 5 by 5 cm tall pieces of wood attached at equal distances along the edge (Fisher et al., 2004). Attached to each cover was a 50 cm long piece of jute that served as a rodent escape string to minimize mortality. The pitfall traps were stocked with two to three small pieces of kibble, a 12 cm long by 5 cm diameter PVC pipe piece lined with small amounts of batting, and a 3-5 cm piece of wet sponge to keep trapped animals hydrated (Karraker, 2001; Persons and Nowak, 2006). When the wet sponge attracted ants it was temporarily removed (Fisher et al., 2004). When in use, traps were checked every 12 hours. When not in use, the bucket lid was securely fastened, rocks placed on the lid, and soil placed loosely over the lid to seal the trap.

Each bucket trap was separated by 7.5 m of 30 cm tall tan cloth drift fencing, which guided reptiles differentially into traps from burned and unburned habitats. Each array was arranged in a zigzag pattern, providing more intercept angles (Fisher et al., 2004). The buckets were completely fenced on three sides, with three buckets fenced on the patch side and three buckets fenced on the burn side (Figure 3). This design allowed for the study of directional movement, as individuals captured in buckets fenced on the patch side came from the burn area and individuals captured in buckets fenced on the burn side were moving away from the patch. The fencing was held in place by wooden stakes and buried 7-12 cm into the ground.

The array and trap numbers of all captured lizards were recorded. A small tissue sample was taken from the tail tip and preserved in 95% ethanol for possible later genetic analysis (Hirsch et al., 2002). For easy recognition of an individual from a distance captured lizards were marked, based on their site location, with nail polish. Because they were captured in higher numbers, *Uta stansburiana* (side-blotched lizard) were also marked by toe clipping one digit (Ferner, 1979; Swingland, 1978). Small mammals (that did not escape via the escape string) and captured invertebrates were recorded to species and family, respectively. No mortalities occurred during the course of this study and all individuals were released at the site of capture.

Trapping was conducted on a monthly basis, between temperatures of 2-42°C. Traps were closed during heavy rains and when temperatures reached 0°C to prevent mortality. Trap effort for this study was defined as the number of open traps per trap session, with a session being 12 hours. Trap effort was 5,324 trap days/nights (7 arrays x 6 buckets in each array x 135 trap sessions-346 trap closures due to unforeseen circumstances).

Statistical Analysis

A Shapiro-Wilk test for normality was conducted, and when data were not normally distributed transformations using $\log(x)$, $\ln(x)$, x^2, and $\sqrt{x}$ were performed. Analyses involving herpetological community structure were conducted using PRIMER. All other analyses were completed using PRISM statistical software.

The mean, standard deviation, and minimum/maximum temperatures were calculated for temperature data. Air and ground surface temperatures in warm (May-August 2006 and 2007) and cold seasons (September-October 2006 and March-April 2007) were analyzed using paired *t*-tests.

Vegetation data were analyzed using χ^2, with the means and standard deviations of each plant height class calculated to compare plant heights in burned and unburned areas.

The observation rate of reptile species seen during transect surveys was calculated. ANOSIM (analysis of similarity) of species diversity between years and in burned and vegetated habitats and SIMPER (similarity percentages) analyses were conducted (Clarke, 1993). Transect data collected on *U. stansburiana* locations by line segment through time in each habitat type were analyzed using Friedman randomized block test, χ^2, and Fisher's Exact tests.

The capture rate of each lizard species caught during pitfall trapping was calculated along with the recapture rate for *U. stansburiana*. ANOSIM and SIMPER analyses were conducted to determine dominance in the herpetological community. Abundance data collected on trapped *U. stansburiana* were analyzed with a paired *t*-test and a Fisher's Exact test. Species of mammal and family of invertebrate captured were also tallied.

RESULTS

Ambient Air, Ground Surface, and Subterranean Temperatures

The mean ambient air temperature (±*SD*) for the 2006 and 2007 warm seasons combined was 31.1 ± 5.0ºC and for cold seasons was 20.6 ± 7.2ºC. Ambient air temperatures in the warm season of 2007 were significantly higher than 2006 ($t = 5.420$, $df = 195$, $p < 0.0001$, $\bar{x}$ 2006 = 29.6 ± 5.1, $\bar{x}$ 2007 = 32.4 ± 4.5). The means of the cold seasons were not significantly different ($t = 0.3196$, $df = 55$, $p = 0.7505$, $\bar{x} = 20.6 \pm 7.2$) from one another (Figure 4a).

Ground surface temperature data for 2006 and 2007 were divided by habitat type, season, and year creating data sets for 2006 and 2007 of warm season unburned, warm season burned, cold season unburned, and cold season burned. Unburned habitats were not found to be significantly different between years in the warm season ($t = 0.0206$, $df = 194$, $p = 0.9836$, $\bar{x} = 31.5 \pm 5.9$). Significant differences were found in the cold season ($t = 3.570$, $df = 55$, $p = 0.0007$, $\bar{x}$ 2006 = 19.3 ± 5.2, $\bar{x}$ 2007 = 16.7 ± 6.9), with 2006 being warmer. In burned habitat significant differences were not found between years in the warm season ($t = 1.091$, $df = 193$, $p = 0.2767$, $\bar{x} = 32.5 \pm 6.1$), while the 2006 cold season showed a significant difference in means between years ($t = 8.877$, $df = 52$, $p < 0.0001$, $\bar{x}$ 2006 = 19.5 ± 5.6, $\bar{x}$ 2007 = 17.5 ± 7.0). Also, burned habitats in the warm season had significantly higher temperatures ($t = 11.61$, $df = 415$, $p < 0.0001$, $\bar{x}$ unburned = 31.5 ± 5.9, $\bar{x}$ burned = 32.5 ± 6.0) than unburned. The cold season ($t = 0.6167$, $df = 112$, $p = 0.5387$, $\bar{x} = 18.2 \pm 6.3$) did not have significantly higher temperatures in burned habitats (Figure 4b).

Subterranean temperatures in the warm season of 2007 were significantly higher in both habitat types (unburned $t = 2.003$, $df = 195$, $p = 0.0466$, $\bar{x}$ 2006 = 30.6 ± 8.2, $\bar{x}$ 2007 = 31.2 ± 5.6, and burned $t = 2.239$, $df = 195$, $p = 0.0263$, $\bar{x}$ 2006 = 32.4 ± 8.3, $\bar{x} = 32.8 \pm 5.4$). I found that 2006 was significantly colder in the cold seasons in both habitats (unburned $t = 10.61$, $df = 55$, $p<0.0001$, $\bar{x}$ 2006 = 15.2 ± 4.5, $\bar{x}$ 2007 = 11.9 ± 6.4, and burned $t = 9.739$, $df = 55$, $p < 0.0001$, $\bar{x}$ 2006 = 15.7 ± 4.1, $\bar{x}$ 2007 = 12.6 ± 6.2). In the warm season subterranean temperatures in the burned area were significantly higher than in the unburned area ($t = 50.08$, $df = 417$, $p < 0.0001$, $\bar{x}$ unburned = 30.9 ± 6.9, $\bar{x}$ burned = 32.6 ± 6.9). Subterranean temperatures in burned habitats were also higher in the cold season ($t = 7.641$, $df = 111$, $p < 0.0001$, $\bar{x}$ unburned = 13.5 ± 5.5, $\bar{x}$ burned = 14.2 ± 5.1) during this study (Figure 4c).

During pitfall trapping the minimum air temperature recorded was 0ºC and the maximum temperature was 42ºC.

Vegetation Point-Intercept Transect Surveys

I found that only counts of plants <10 cm tall at one site in the burned area along the fire perimeter and one site in the burned area around a habitat patch, were normally distributed. The total number of plants in the unburned areas (1,440; 68.58% total cover) was higher than in burned areas (846; 40.28% total cover). There were differences in the distribution of vegetation heights in each habitat ($\chi^2 = 389.9$, $df = 1$, $p < 0.0001$). There were significantly more plants in the burned area under 10 cm than in any other height class in either habitat (Table 3). The number of plants in burned areas in this height class increased from 2006-2007 (264 and 345 total plants). For all heights, except <10 cm, unburned habitats had more plants per site than burned. Although all plants seen were not recorded to species, of those recorded 2% and 21% were noted as *Erodium cicutarium* or a grass species in unburned areas. In burned areas this trend was reversed with *E. cicutarium* accounting for 31% and grasses making up only 7%.

Reptile Transect Surveys

During transect surveys five lizard and one snake species were observed (Table 4). Multi dimensional scaling (MDS) showed that transect sites clustered together by habitat type with the exception of two sites; one unburned patch and one burned perimeter transect location. These two sites were removed from the analysis because they had significantly more zero values and were outliers that made it impossible to determine how locations clustered. I found no significant differences in the species assemblages between years (ANOSIM, $R = 0.018$, $p = 0.271$ and $R = -0.043$, $p = 0.888$) or between unburned and burned habitats ($R = 0.053$, $p = 0.109$ and $R = 0.010$, $p = 0.333$) along the perimeter and in the patch locations, respectively. Therefore, data from 2006 and 2007 were combined and reanalyzed using ANOSIM. Species found at perimeter and patch sites did not differ significantly ($R = 0.038$, $p = 0.272$); however, differences were found ($R = 0.220$, $p = 0.022$) between unburned and burned locations. A SIMPER analysis showed that in the unburned areas, *U. stansburiana* accounted for 88.0% of individuals, with *A. tigris* and *S. occidentalis* making up 14.7% and 13.5% of individuals, respectively. In the burned areas *U. stansburiana* comprised 98.6% of individuals.

U. stansburiana abundance data were not normally distributed and a normalizing transformation could not be found. A Friedman randomized block test found no significant differences in the number of individuals seen by segment location along transects in each habitat type through time (Friedman statistic = 6.500, $p = 0.0897$). Differences were found between habitat types ($\chi^2 = 9.952$, $df = 3$, $p = 0.0190$). Burned areas around patches in 2006 and outside the perimeter in 2007 had the fewest individuals. Most *U. stansburiana* were recorded in burned areas along perimeter sites in 2006, followed by unburned patch sites in 2007 (Figure 5). Although combining perimeter and patch sites yielded more individuals found in unburned habitat ($n = 77$ compared to $n = 62$), there were no significant differences in the number of *U. stansburiana* in unburned and burned habitats (Fisher's Exact test; $p = 0.0624$). Also, no detectable differences were found when year data were combined (Fisher's Exact test; $p = 0.1201$), although burned patches had the fewest ($n = 22$), while burned perimeter and unburned patch habitats had the most individuals (both had $n = 39$). Surprisingly, significant differences were found when unburned and burned sites along the perimeter and at patch locations were combined (Fisher's Exact test; $p = 0.0258$).

Pitfall Trapping

During pitfall trapping six lizard species were captured (Table 5). MDS showed that pitfall trap sites clustered together by year with the exception of one site in a patch location in 2006, which had more zero data points than other sites. This site was removed in order to see patterns in the remaining data. Species abundance did differ significantly between years (ANOSIM, $R = 0.216$, $p = 0.044$). More individuals were captured in 2007 ($n = 60$) than 2006 ($n = 36$). Also, 2006 had one single species not captured in 2007, while 2007 had two that were not present in 2006. *U. stansburiana* dominated the herpetofaunal assemblages in both years; however, this species was represented in a higher percentage in the 2007 (SIMPER, 2006 = 92.6% and 2007 = 98.2%).

Of the 80 *U. stansburiana* captured over the course of this study, 19 were recaptures, resulting in a recapture rate of 23.75%. In 2006 there were very few recaptures (10.71%); however, 2007 saw an increase in recaptured individuals (30.77%). Recaptures of individuals were removed from statistical analyses. The total number of *U. stansburiana* captured by site were normally distributed in both years (2006 $p = 0.2601$ and 2007 $p = 0.7222$). No significant differences in the number of individuals caught between years ($t = 1.135$, $df = 12$, $p = 0.2787$) was found. No significant differences in the direction of movement of individuals was found when these data were combined for analysis (Fisher's Exact test; $df = 4$, $p = 0.2968$), even though the number of *U. stansburiana* moving into patches actually doubled (9 to 18) from 2006-2007 (Figure 6). During trapping more juveniles were captured (66%) than adults (34%), with most *U. stansburiana* being captured in 2007.

I also recorded the numbers of mammals and invertebrates captured in pitfall traps. As these individuals could easily climb the drift fencing their direction of movement could not be determined. Interestingly, the number of mammalian species captured decreased, as did the total number of individuals captured from the first to the second year (Table 6). Conversely, the number of invertebrate families and the total number of individuals captured increased from 2006-2007 (Table 7).

DISCUSSION

Temperature and Vegetation

Due to air temperature variation, 2007 was warmer than 2006, but both ground surface and subterranean temperatures were higher in burned areas than in unburned areas in both years.

The plant community in unburned areas had almost 30% more cover than burned areas and remained relatively stable through time. However, the burned areas had more than twice the number of plants in the <10 cm height class, and very few grew to over 10 cm during the course of this study. This indicates that most were low growing ground cover species. This is consistent with long term studies of plant communities in the Southwest that have found areas affected by wildfire are rapidly colonized by low growing ground cover species that are predominantly alien (Brooks, 2002; Brooks and Matchett, 2003). Additionally, soil nutrient research in the Mojave found that grasses were better competitors and often become dominant following disturbance (Brooks, 1999).

Comparison of Transect and Pitfall Data

Transect and pitfall surveys had comparable species diversity with each other. *Uta stansburiana* was the dominant species in all locations. I found the highest number along the fire perimeter on the burned side in 2006, which is similar to a study conducted after a wildfire in Arizona that found reptiles exhibited a preference for disturbed sites (Cunningham et al., 2002). However, in 2007 the number of individuals found in this area decreased by more than half. It may be that individuals utilized this area more heavily initially because the higher ground temperatures allowed for optimal basking sites. In 2007 temperatures may have become too high creating a less than ideal habitat type that did not provide a thermoregulatory gradient or enough cover (Wilson, 1991). The number of *U. stansburiana* in unburned perimeter locations was relatively constant through time, indicating that this population was the most stable. The numbers found at patches increased in burned and unburned areas, with unburned sites having more individuals.

The directional design of the pitfall arrays allowed me to assess whether individuals were moving into or out of habitat patches. However, no directional pattern was detected, likely because of the low numbers of individuals captured. However, in 2006 the number of *U. stansburiana* captured in pitfall traps at patch sites (n = 28) was comparable to the number seen during transect surveys at the same locations (n = 25). In 2007 more were captured (n = 52) than seen (n = 37). It may be that the increased temperatures in 2007 altered the movements of *U. stansburiana*, decreasing their daily activity.

Future Research Recommendations

This research would have benefited from a longer study period. Two years is not a sufficient amount of time to accurately determine trends in a fragmented system that is undergoing post-wildfire successional stages. Many environmental parameters, including yearly temperature and rainfall fluctuations, could account for the trends seen and result in notable year-to-year variability (Hirsch et al., 2002).

Conservation Implications

Although the results of a study conducted in a single location and affected by a single event may not be fully extrapolated to other locations or events, it is clear that wildfire is a serious threat to biodiversity in the Mojave. The effects of large desert fires are poorly understood, largely because this is a relatively new problem (Brooks, 2002; Brooks and Matchett, 2003). Information on floral community succession and faunal survival is useful to help understand the long-term consequences of altering landscapes, and could lead to increased control of invasive species. These species have created a positive feedback system, or a grass-fire cycle, in the Mojave. The resulting habitats are increasingly homogeneous, and provide few resources (Esque, 1999; Esque et al., 2003; Valentine et al., 2007).

The presence of *U. stansburiana* is a good indicator of the possible establishment of healthy populations of many other species. *U. stansburiana* is an abundant and widespread lizard that is a food source for many species that cannot reoccupy an area until suitable numbers of prey are present (Stebbins, 2003). Low numbers will negatively impact the community, decreasing both diversity and abundance. This study suggests that wildfire in the Mojave negatively affects the reptile community.

Due to the hostile conditions and already limited resources, desert environments are not able to maintain dense populations of wildlife, creating fragile systems composed of highly specialized species. Deserts, although coming under increasing pressure from human expansion and activities, are some of the most inhospitable and therefore remote and unexploited areas in the continental United States. Wildlands are becoming increasingly rare worldwide and few ecosystems contain organisms with such unique adaptations to extreme conditions as desert regions, making conservation in these areas a critical concern.

TABLE 1. Transect Locationss in the Hackberry Region, Mojave National Preserve

Site	Starting Easting	Starting Northing	Ending Easting	Ending Northing	Elevation (m)
Patch 1	645412	3892561	645405	3892517	1596
	645409	3892565	645438	3892531	
	645431	3892589	645438	3892543	
Patch 2	645425	3892203	645476	3892204	1591
	645422	3892195	645470	3892178	
	645438	3892181	645467	3892157	
Patch 3	642829	3887189	642812	3887237	1661
	642821	3887185	642789	3887221	
	642806	3887173	642777	3887208	
Patch 4	642810	3887316	642814	3887365	1665
	642786	3887307	642798	3887350	
	642754	3887298	642787	3887342	
Patch 5	642814	3887533	642841	3887575	1670
	642788	3887525	642821	3887566	
	642708	3887531	642806	3887571	
Patch 6	645913	3887650	642933	3887695	1684
	642929	3887649	642944	3887699	
	642954	3887662	642962	3887709	
Patch 7	643023	3887958	643039	3887909	1679
	643050	3887969	643049	3887917	
	643077	3887972	643063	3887927	
Perimeter 1	646600	3892811	646555	3892819	1594
	646598	3892786	646549	3892794	
	646586	3892763	646540	3892786	
Perimeter 2	646545	3892659	646493	3892658	1604
	646552	3892636	646500	3892638	
	646536	3892610	646488	3892620	
Perimeter 3	646524	3892565	646480	3892567	1656
	646522	3892553	646480	3892546	
	646538	3892529	646492	3892526	
Perimeter 4	646513	3892468	646465	3892474	1660
	646506	389245	646457	3892448	
	646498	3892431	646458	3892678	
Perimeter 5	646586	3892634	646587	3892681	1580
	646595	3892616	646611	3892668	
	646623	3892625	646623	3892678	
Perimeter 6	645283	3892595	645259	3893556	1582
	645262	3892604	645247	3893560	
	645244	3892615	645237	3893568	
Perimeter 7	645167	3893604	645186	3893568	1580
	645153	3893610	645175	3893571	
	645132	3893600	645150	3893554	

Note: All locations in map datum NAD83, UTM zone 11.

TABLE 2. Locations of Pitfall Trap Arrays in the Hackberry Region of the Mojave National Preserve

Array	Easting	Northing	Elevation (m)
1	645395	3892528	1596
2	645456	3892203	1591
3	642811	3887222	1661
4	642804	3887343	1665
5	642873	3887558	1670
6	642942	3887683	1684
7	643035	3887924	1679

Note: All locations in map datum NAD83, UTM zone 11.

TABLE 3. Percent Vegetation Cover in Unburned and Burned habitats by Height Class

Height Class (cm)	Unburned		Burned	
	Number	Percent Cover	Number	Percent Cover
<10	220	10.48	631	30.05
10-30	295	14.05	133	6.33
30-50	248	11.81	63	3.00
50-100	345	16.43	16	0.76
>100	332	15.81	3	0.14
Total	1440	68.58	846	40.28

TABLE 4. Reptile Species Observed During Transect Surveys

Species	2006		2007		Unburned		Burned	
	Number	Rate	Number	Rate	Number	Rate	Number	Rate
Aspidocelus tigris Western whiptail	7	0.3684	4	0.2105	11	0.2895	0	0
Gambelia wislizenii Long-nosed leopard lizard	2	0.1053	0	0	1	0.0263	1	0.0263
Masticophis taeniatus Striped whipsnake	1	0.0526	0	0	0	0	1	0.0263
Phrynosoma platyrhinos Desert horned lizard	0	0	1	0.0526	0	0	1	0.0263
Sceloporus occidentalis Western fence lizard	8	0.4211	7	0.3684	5	0.1316	10	0.2632
Uta stansburiana Side-blotched lizard	80	4.2105	56	2.9474	75	1.9737	61	1.6053
Total	98	5.1579	68	3.5789	92	2.4211	74	1.7105

Note: Observation rates were calculated using number of observations/number of transects conducted (Persons and Nowak, 2006).

TABLE 5. Reptile Species Captured During Pitfall Trapping

Species	2006		2007	
	Number	Capture Rate	Number	Capture Rate
Aspidocelus tigris Western whiptail	5	0.0725	1	0.0145
Gambelia wislizenii Long-nosed leopard lizard	1	0.0145	0	0
Sceloporus magister Desert spiny lizard	0	0	3	0.0435
Sceloporus occidentalis Western fence lizard	2	0.0290	5	0.0435
Uta stansburiana Side-blotched lizard	28	0.4056	52	0.7536
Xantusia vigilis Desert night lizard	0	0	1	0.0145
Total	36	0.5216	62	0.8969

Note: Capture rates were calculated using number of captures/number of pitfall trap sessions conducted (Persons and Nowak, 2006).

TABLE 6. Mammal Species Captured During Pitfall Trapping

Species	2006	2007
Dipodomys deserti Desert kangaroo rat	6	3
Lagurus curtatus Sagebrush vole	3	0
Perognathus longimembris Little pocket mouse	1	1
Perognathus penicillatus Desert pocket mouse	0	1
Peromyscus sp. Pygmy mouse species	3	0
Thomomys bottae Valley pocket gopher	1	1
Total Number of Individuals	14	6
Total Number of Species	5	4

TABLE 7. Invertebrate Families Captured During Pitfall Trapping

Family	2006	2007
Caraboctonidae (Desert scorpions)	35	71
Cerambycidae (Long-horned beetles)	0	1
Cicadidae (Cicadas)	0	1
Eremobatidae (Windscorpions)	31	35
Gryllacrididae (Camel crickets)	98	152
Gryllidae (Crickets)	3	0
Mantidae (Mantids)	1	1
Mutillidae (Velvet ants)	0	2
Myrmeleontidae (Antlions)	0	1
Pompilidae (Tarantula hawks)	0	1
Reduviidae (Assassin bugs)	0	13
Scolopendridae (Multicolored centipedes)	2	0
Tenebrionidae (Darkling beetles)	483	623
Theraphosidae (Blonde tarantulas)	0	1
Total Number of Individuals	653	902
Total Number of Families	7	12

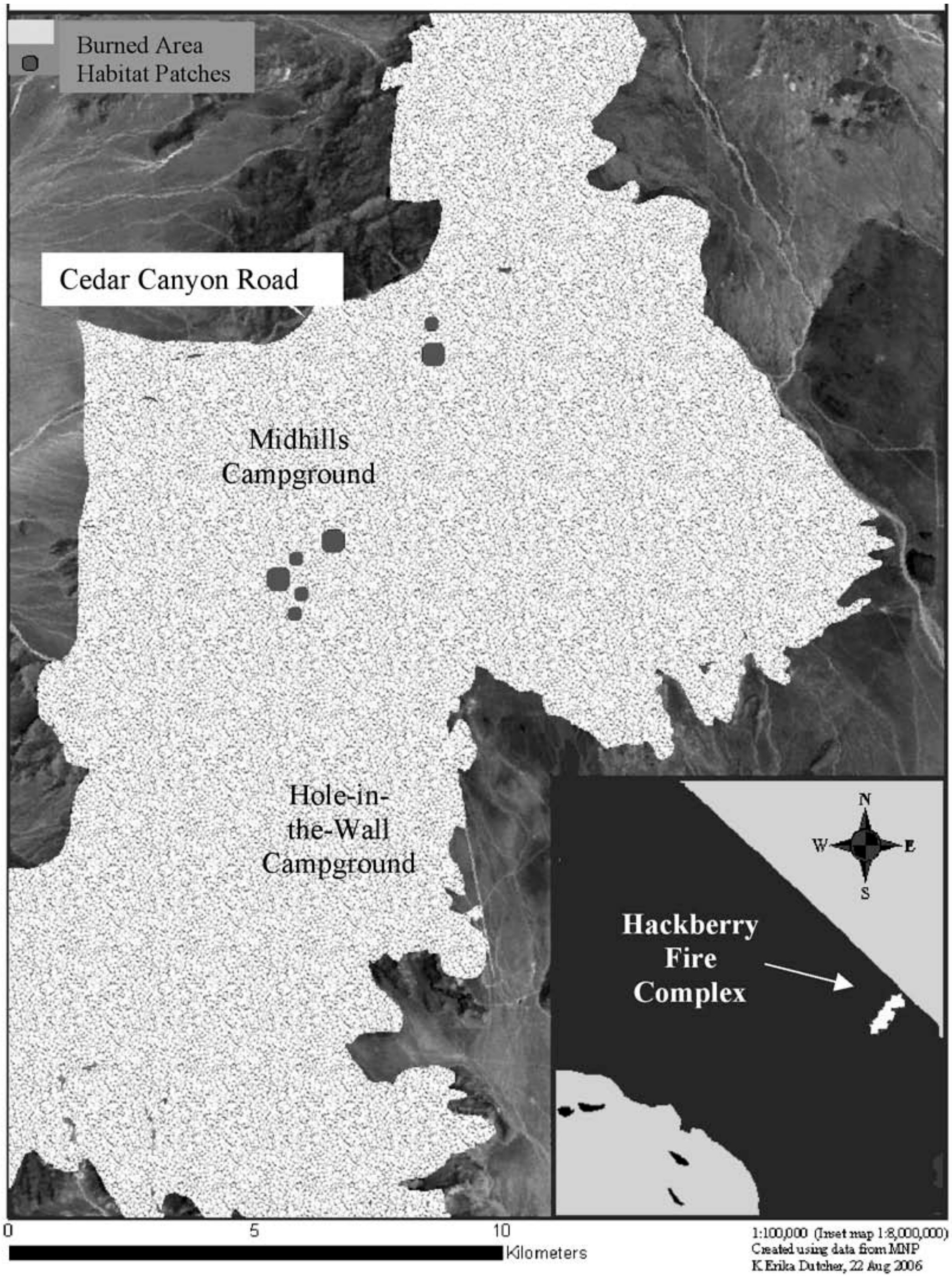

FIGURE 1. Habitat patch locations within the Hackberry region of the Mojave National Preserve. Habitat patch size not to scale. The subset map shows the location of the Hackberry wildfire in Southern California. Map created by K. Erika Dutcher and Dr. D. Underwood using data from the National Park Service, 2006.

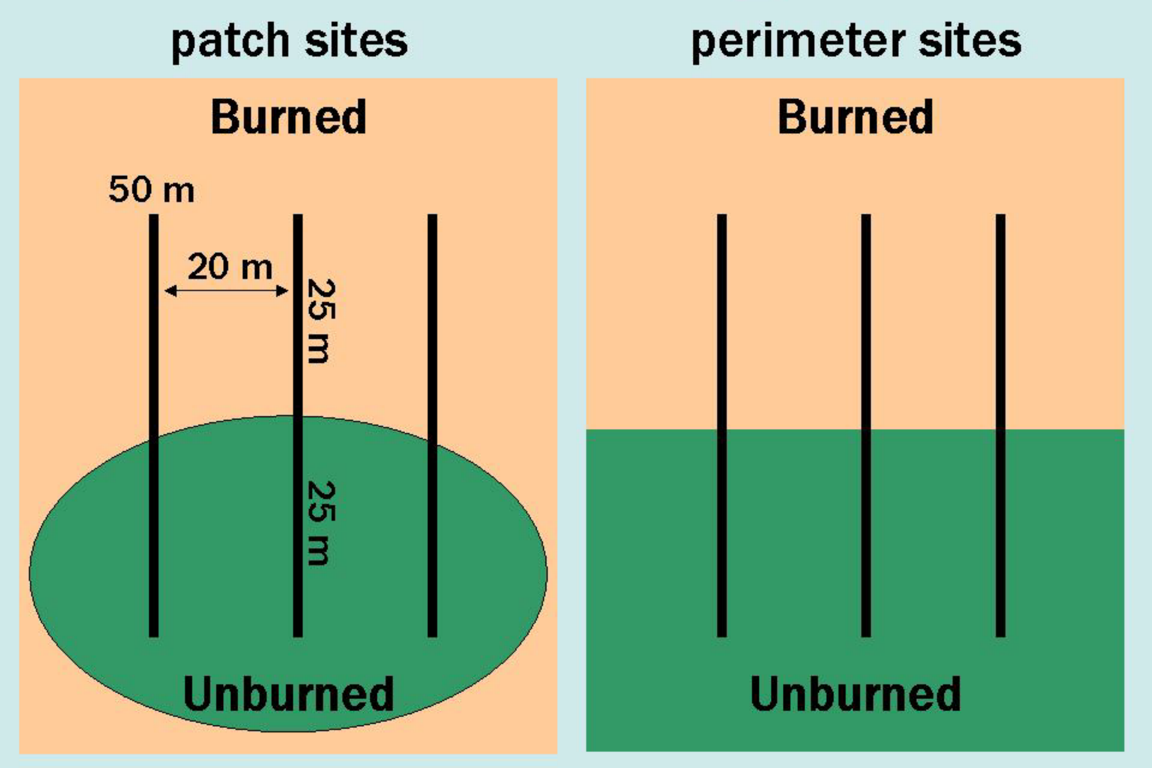

FIGURE 2. Transect design. Each site had three 50 m transects separated by 20 m. Half (25 m) of each transect was located in burned habitat and 25 m in unburned habitat.

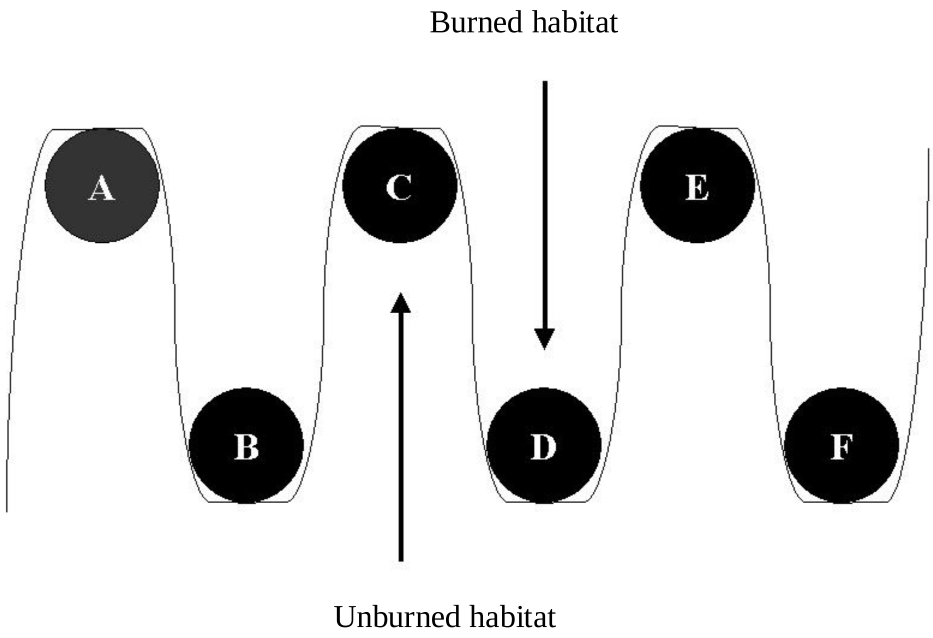

FIGURE 3. Pitfall array design. Buckets were fenced on three sides to prevent reptiles from the burned area entering traps A, C, and E and reptiles from the unburned area entering traps B, D, and F.

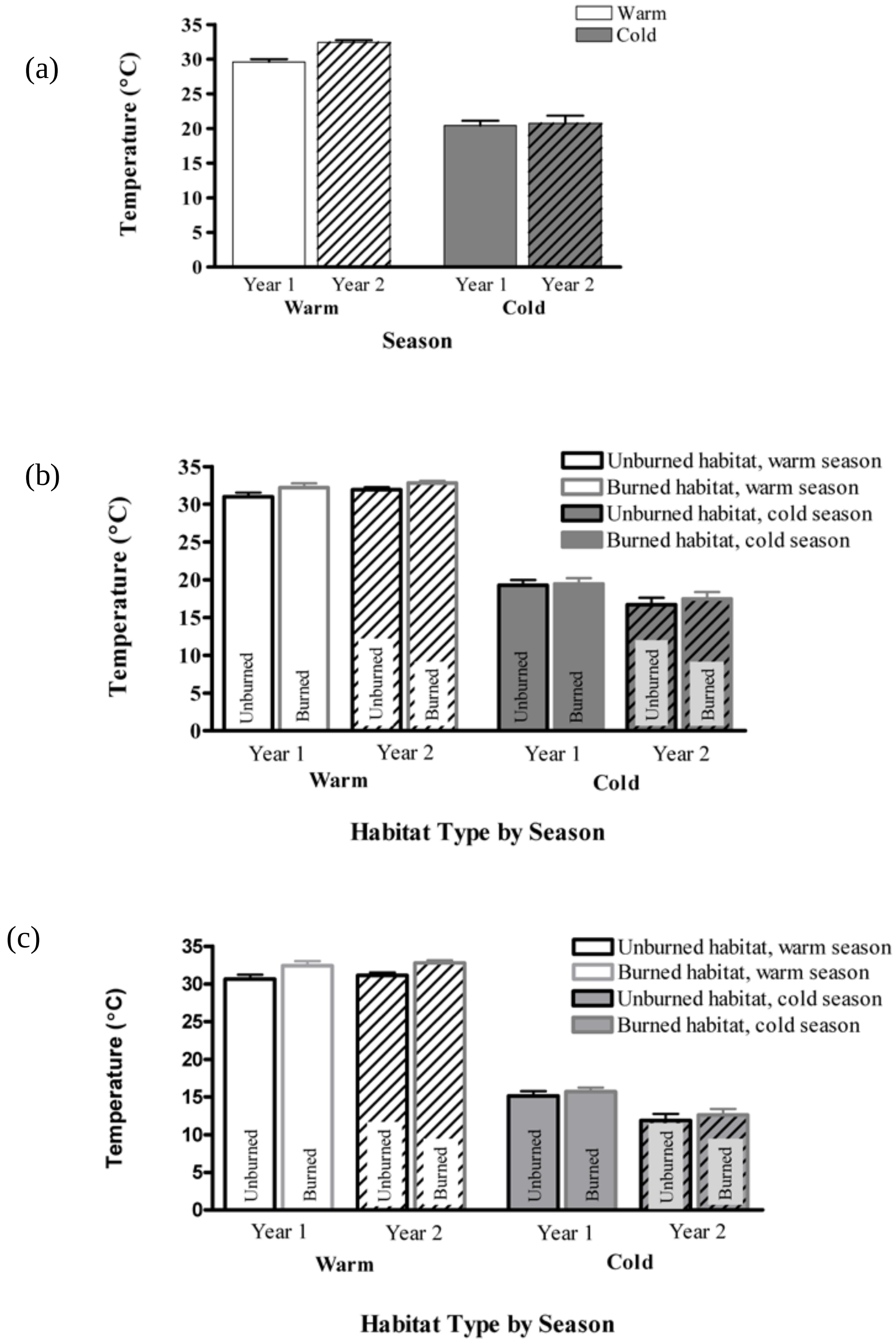

FIGURE 4. Ambient, ground, and subterranean temperatures ($\bar{x}$ ± SD). (a) Average ambient temperatures by year in the warm and cold seasons. (b) Average ground temperatures for unburned and burned habitats by year in each season. (c) Average subterranean temperatures for both habitats by year in each season.

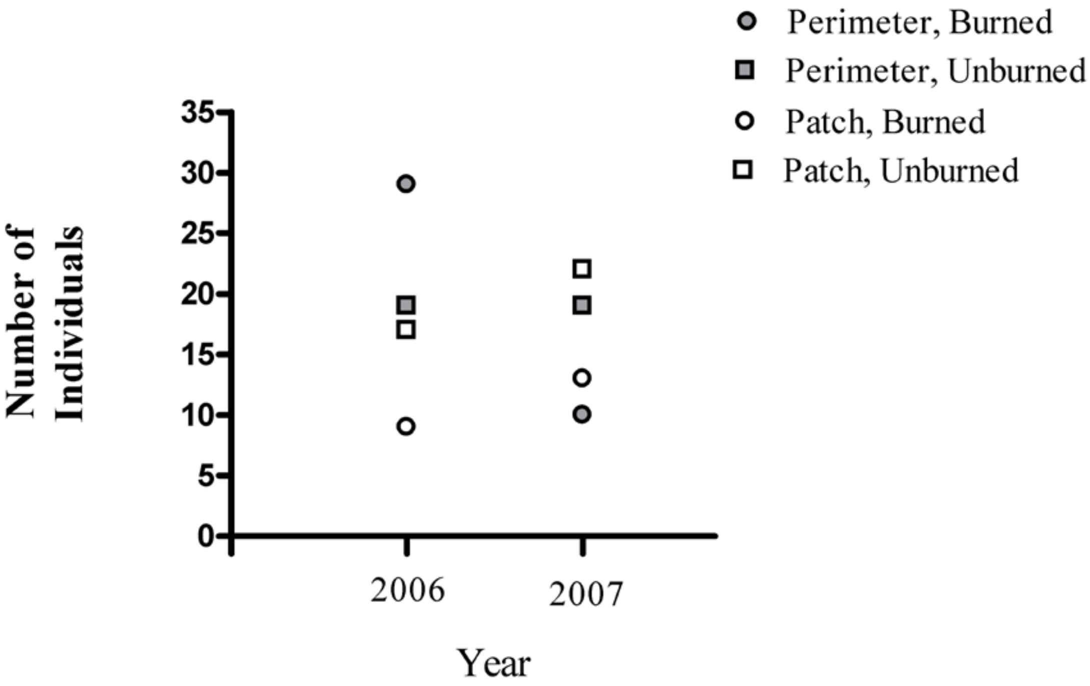

FIGURE 5. Total number of *Uta stansburiana* observed during transect surveys in each habitat type by year.

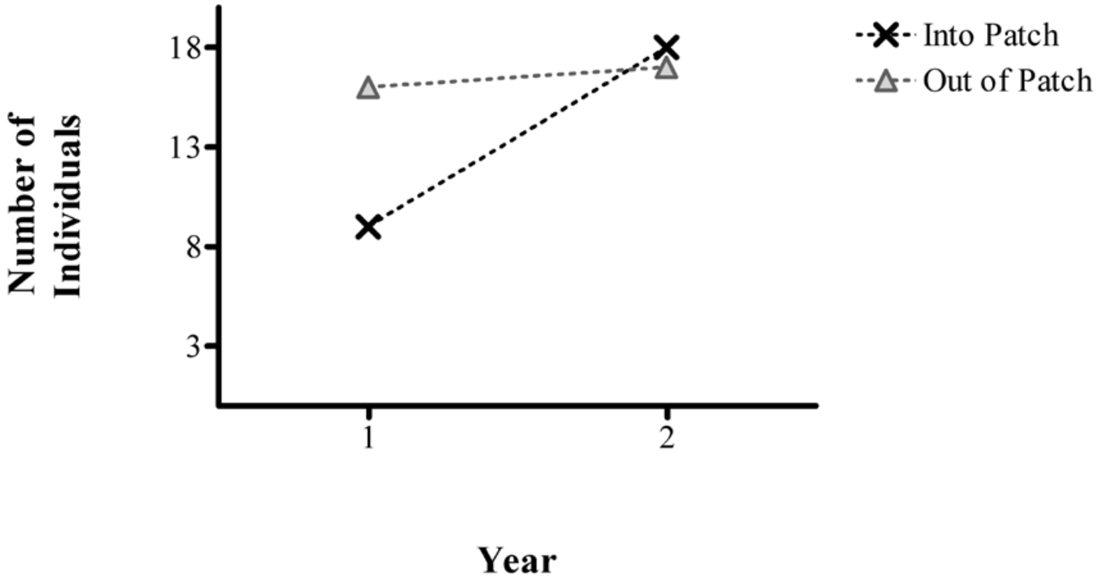

FIGURE 6. Total number of *Uta stansburiana* captured in pitfall traps moving into or out of habitat patches by year. Recaptured individuals were removed from the totals.

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FIRE EFFECTS ON SEED BANKS AND VEGETATION IN THE EASTERN MOJAVE DESERT: IMPLICATIONS FOR POST-FIRE MANAGEMENT

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INTRODUCTION

Limited information is currently available on the short-term effects of fire on soil seed banks and vegetation in the Mojave Desert. This information is critical for determining if postfire seedings are potentially beneficial, or even necessary, in this ecosystem. Of all the management tools, aerial seeding is potentially the most cost-effective over large areas because it requires the least amount of lead time. There are clearly many questions associated with this technology, but the more immediate question is whether seeding treatments are necessary in the first place. This question hinges on understanding the short-term effects of fire on the abundance and species composition of soil seed banks and germinated plants immediately following the 70,736 acre Hackberry Fire Complex which occurred at the Mojave National Preserve in the eastern Mojave Desert during late June 2005. Support for this project was provided by the Joint Fire Science Program (project #06-1-2-02).

METHODS

Six sites in the Hackberry Fire Complex were used as replicate sampling blocks, each containing one burned and one unburned experimental unit with 5 non-overlapping sampling units randomly established inside each. This randomized blocks study design consists of 6 blocks X 2 fire treatments X 5 sampling units = 60 total sampling plots. Sampling plots were set up in October 2005 and consisted of a 5 x 30m FMH brush belt transect (USDI National Park Service 2003), overlaid with a 20 x 50m modified Whittaker plot (Stohlgren et al. 1995). Burn severity measurements were collected on the brush belt transects, following FMH protocols (USDI National Park Service 2003). Four 6cm diameter x 3cm deep (volume = 85cm^3) soil samples were collected at each corner of the brush belt transect for determination of seed bank density and species richness and composited into a single soil sample. A ½ cup (111cm^3) portion was grown in a greenhouse during winter 2005-06 following methods adapted from Brenchley and Warington (1939) and modified by Young and Evans (1975). Seed bank density and species richness were measured by counting the number of germinated seedlings for each species.

Above-ground density, cover, and species richness of herbaceous and woody plants were measured during the phenological peak for annual plants in April and early May, 2006, following National Park Service FMH protocols (USDI National Park Service 2003). Spatially nested modified-Whittaker plots were used to measure plant species richness at 1, 10, 100, and $1{,}000\text{m}^2$ scales. We focus specifically on the results of the seed bank and herbaceous plant sampling.

Data was analyzed as a randomized blocks analysis of variance (ANOVA) statistical model. The predictor variable was fire (burned, unburned). The response variables included seed bank density by groups of plants (non-native, native), above-ground vegetation density by groups, and species diversity of the seed bank and above-ground vegetation. The data was log transformed since it was not normally distributed and analyzed with SAS Proc GLIMMIX.

RESULTS AND DISCUSSION

Seed banks

Total seed bank density was significantly lower in burned (2,494 seeds/m^2) than unburned (12,460 seeds/m^2) areas ($P<0.0001$)(Fig. 1). This translates into a seed bank depletion (mortality) rate of 80%. Recent aerial seedings of postfire landscapes in the Mojave Desert have ranged from 140 seeds/m^2 (13 seeds/ft^2)(Christiana Lund, BLM, pers. comm.) to 646 seeds/m^2 (60 seeds/ft^2) (Karen Prentice, BLM, pers. comm.), and postfire drill seedings are typically applied at a rate of 323 seeds/m^2 (30 seeds/ft^2)(Karen Prentice pers. comm.). If these seeding rates were applied after the Hackberry Fire Complex, they would have only reduced the depletion rate of the seed bank to 79% if 140 seeds/m^2 were added, or 75% if 646 seeds/m^2 were added. To completely ameliorate seed bank depletion rates (to a 0% net loss), 9,966 seeds/m^2 (926 seeds/ft^2) would have to have been added, an increase of 1,543% over the highest aerial seeding rates typically used.

Non-native seed densities (dominated by *Erodium cicutarium*) were significantly lower in burned (345 seeds/m^2) than unburned (5,667 seeds/m^2) areas ($P<0.0001$)(Fig. 1) (94% depletion rate). Native seed densities were also significantly lower in burned (2,012 seeds/m^2) than unburned (6,701 seeds/m^2) areas ($P=0.0020$)(70% depletion rate). Seed bank species richness per 483cm^2 soil sample was significantly lower where burned (3 species) than unburned (6 species) ($P<0.0001$).

Above-ground herbaceous plants

Total herbaceous plant density was significantly lower in burned (107 plants/m^2) than unburned (329 plants/m^2) areas ($P<0.0001$)(Fig. 2). Non-native density was lower in burned (62 plants/m^2) than unburned (156 plants/m^2) areas ($P<0.0001$). Similarly, native density was lower where burned (45 plants/m^2) than unburned (174 plants/m^2) ($P<0.0001$). Thus, plant densities were reduced 67% during the first postfire spring, and these reductions were similar for native and non-native species. Species richness of herbaceous plants was also significantly lower in burned than unburned areas at 1m^2 (7 species vs. 10 species), 10m^2 (14 vs. 16), 100m^2 (27 vs. 30), and 1,000m^2 (40 vs. 45) spatial scales.

SUMMARY AND CONCLUSIONS

These first year results indicate that the Hackberry Fire Complex of June 2005 had the immediate effects of reducing soil seed bank and herbaceous plant density and diversity during the first postfire fall (October 2005) and spring (April-May 2006) respectively. Typical postfire seeding rates for the Mojave Desert would not have resulted in appreciable increases in seed bank densities if they had been applied after this fire, although our data do not allow us to that these differences would have not have been ecologically significant. The broader implications of these results will be better known after we evaluate results from postfire years 2 and 3.

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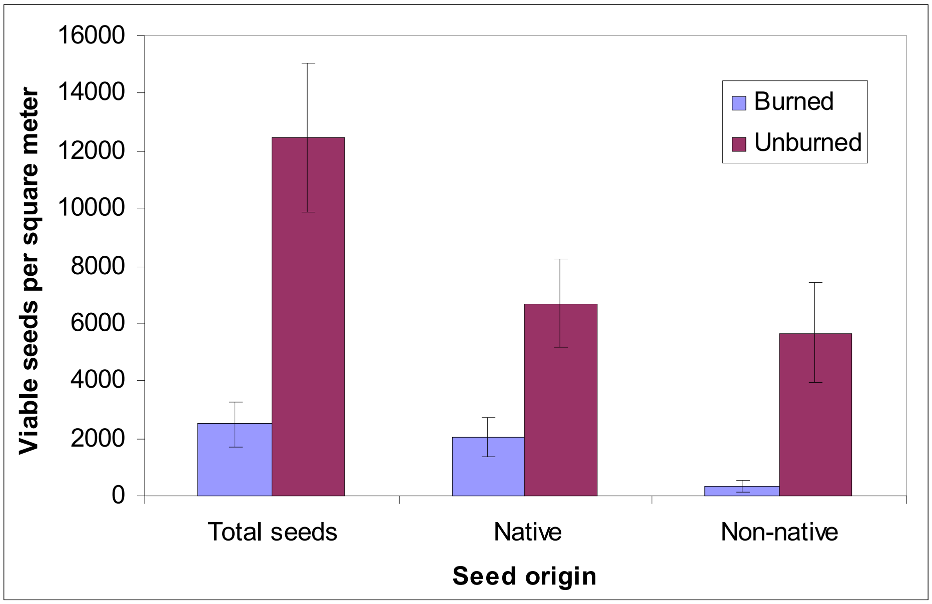

Fig. 1. Density of viable seeds in the seed bank during October 2005 following the June 2005 Hackberry Fire Complex (+/-1 SE, n=6).

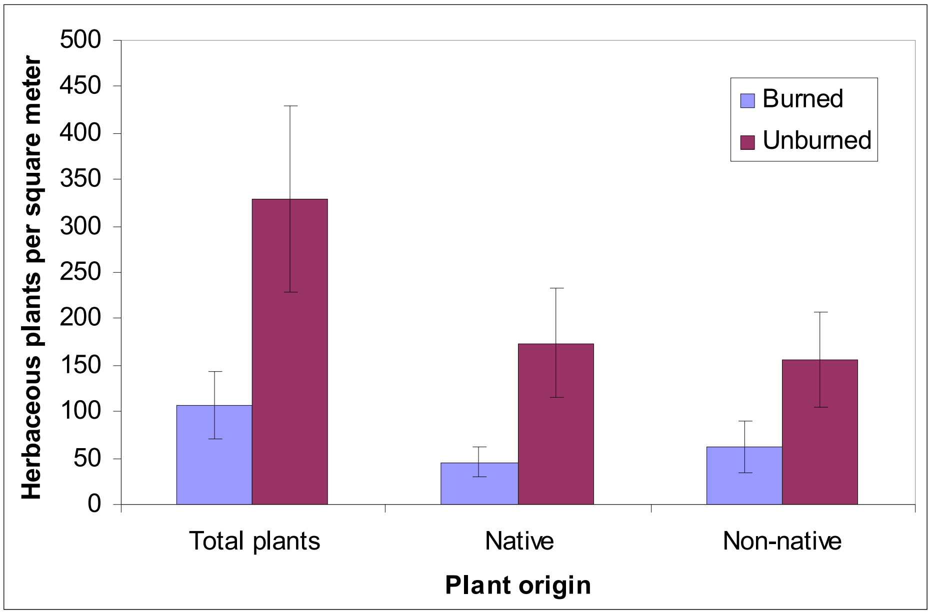

Fig. 2. Herbaceous plant density during April-May 2006 following the June 2005 Hackberry Fire Complex (+/-1SE, n=6).

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A Genetic Assessment of the Recovery Units for the Mojave Population of the Desert Tortoise, *Gopherus agassizii*

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Abstract. – In the 1994 Recovery Plan for the Mojave population of the desert tortoise, *Gopherus agassizii*, the US Fish and Wildlife Service established 6 recovery units by using the best available data on habitat use, behavior, morphology, and genetics. To further assess the validity of the recovery units, we analyzed genetic data by using mitochondrial deoxyribonucleic acid (mtDNA) sequences and nuclear DNA microsatellites. In total, 125 desert tortoises were sampled for mtDNA and 628 for microsatellites from 31 study sites, representing all recovery units and desert regions throughout the Mojave Desert in California and Utah, and the Colorado Desert of California. The mtDNA revealed a great divergence between the Mojave populations west of the Colorado River and those occurring east of the river in the Sonoran Desert of Arizona. Some divergence also occurred between northern and southern populations within the Mojave population. The microsatellites indicated a low frequency of private alleles and a significant correlation between genetic and geographic distance among 31 sample sites, which was consistent with an isolation-by-distance population structure. Regional genetic differentiation was complementary to the recovery units in the Recovery Plan. Most allelic frequencies in the recovery units differed. An assignment test correctly placed most individuals to their recovery unit of origin. Of the 6 recovery units, the Northeastern and the Upper Virgin River units showed the greatest differentiation; these units may have been relatively more isolated than other areas and should be managed accordingly. The Western Mojave Recovery Unit, by using the new genetic data, was redefined along regional boundaries into the Western Mojave, Central Mojave, and Southern Mojave recovery units. Large-scale translocations of tortoises and habitat disturbance throughout the 20th century may have contributed to the observed patterns of regional similarity.

Key Words. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; conservation genetics; distinctive population segment; evolutionary significant unit; management units; microsatellites; mitochondrial DNA; Mojave Desert; USA

The desert tortoise (*Gopherus agassizii*) is a widespread species (or possible species complex) occurring in the southwestern United States and northwestern Mexico (Fritts and Jennings 1994; Berry et al. 2002; Stebbins 2003). The US Fish and Wildlife Service (USFWS) federally listed the species as threatened under the Endangered Species Act, as amended, in the northern one third of its geographic range, specifically, populations living north and west of the Colorado River in the Mojave and Colorado deserts (USFWS 1990; Fig. 1). The listing occurred primarily because of population declines and habitat loss and deterioration, which were attributed to human activities. In recognition of the distinctiveness of the threatened populations, the USFWS developed the *Desert Tortoise (Mojave Population) Recovery Plan* (referred to herein as *Recovery Plan*) (USFWS 1994) and designated 26,087 km^2 of critical habitat (Berry 1997). About 83% of the critical habitat is on land managed by government agencies.

The federal listing of the desert tortoise as a threatened species brought about a redirection of government efforts to recover the species within its 4 southwestern states (California, Arizona, Nevada, and Utah). Several government agencies prepared new long-term management plans or amended older land-use plans to support recovery efforts (Berry 1997), a process that required more than 16 years. The extent of landscape affected by these efforts was significant and included parts of the Mojave Desert and the Colorado Desert (also called western Sonoran Desert). For convenience, the USFWS termed the populations within critical habitat as the "Mojave" population, when in fact they occur in both the Mojave and Colorado deserts. Herein, we follow this terminology. For populations in the Sonoran Desert of Arizona, we use "Sonoran" populations.

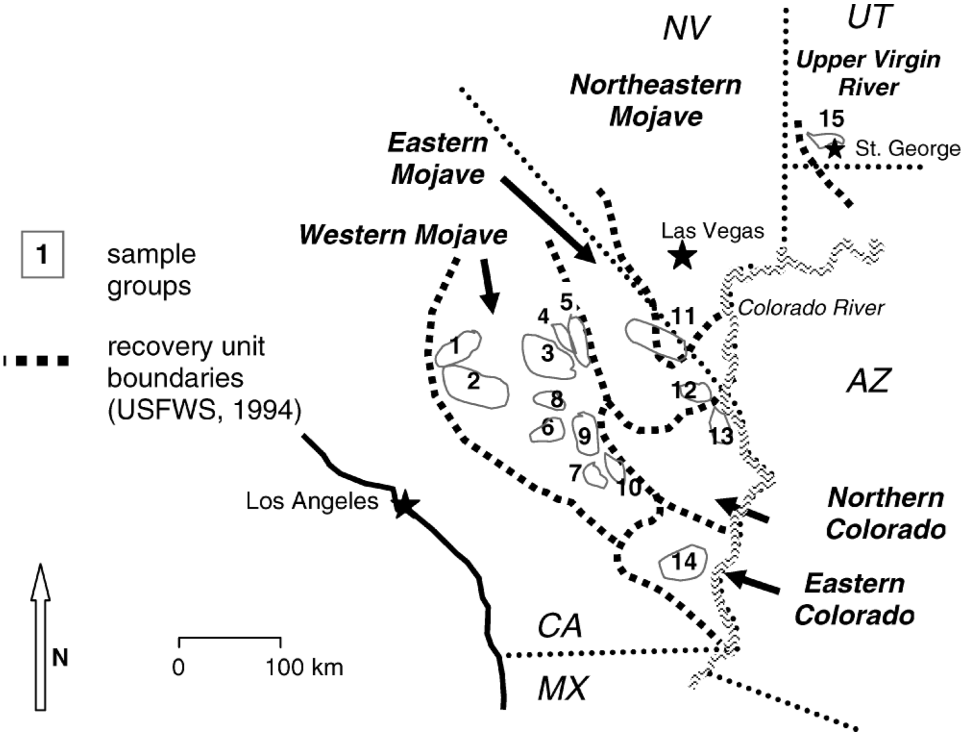

Figure 1. Sample groups and recovery unit boundaries for *Gopherus agassizii* as described in the *Desert Tortoise (Mojave Population) Recovery Plan* (USFWS 1994) and sample sites for this study. Because of their geographic proximity, 3 tortoises from the Eastern Mojave Recovery Unit were combined with 57 tortoises from the Northeastern Mojave Recovery Unit to form sample group 11.

Desert tortoises exhibit substantial differences in morphology (Weinstein and Berry 1987; Germano 1993), physiology (Turner et al. 1986; Wallis et al. 1999; Averill-Murray 2002; Averill-Murray et al. 2002a, 2002b; McLuckie and Fridell 2002), behavior (e.g., Woodbury and Hardy 1948; Burge 1977; Averill-Murray et al. 2002b; Jennings 2002), and genetics (Lamb et al. 1989; Lamb and Lydeard 1994; McLuckie et al. 1999; Lamb and McLuckie 2002) throughout the geographic range in the United States. This variation occurs within and between the Mojave and Sonoran populations.

The authors of the *Recovery Plan* recommended protection of 6 evolutionarily significant units (ESUs) or distinct population segments (DPSs) in 6 "recovery units" (Ryder 1986; Waples 1991, 1998; US Department of the Interior and US Department of Commerce 1996). They noted that the ESUs (or DPSs) consisted of "populations or groups of populations that show significant differentiation in genetics, morphology, ecology or behavior . . . and thus are important components of the evolutionary legacy of *Gopherus agassizii*" (USFWS 1994). They stated that the conservation of all ESUs would help to ensure that "the dynamic process of evolution [in this species] will not be unduly constrained in the future [Waples 1991]" (USFWS 1994). It is important to note that the authors used the phrases ESUs, DPSs, and recovery units synonymously, and their intent was to draw on multiple criteria to delineate units (after Waples 1991, and similar to Crandall et al. 2000). The USFWS also recommended that concepts in the *Recovery Plan* be subjected to hypothesis-testing. In the case of genetics, the limited available mitochondrial deoxyribonucleic acid (mtDNA) data suggested that *G. agassizii* might be composed of more than 1 species, with the Colorado River acting as a boundary in the northern part of the geographic range (Lamb et al. 1989; summarized in Berry et al. 2002).

Since the *Recovery Plan* (USFWS 1994) was published, the fields of population and conservation genetics have advanced rapidly. Numerous new, powerful techniques are now available for processing, statistically analyzing, and interpreting genetic samples (e.g., DeSalle and Amato 2004; Pearse and Crandall 2004; Manel et al. 2005; Allendorf and Luikart 2007). In 1996, the federal government further clarified the Endangered Species policy on DPSs for vertebrates (US Department of the Interior and US Department of Commerce 1996). The academic dialog on the definitions and applicabilities of ESUs, DPSs, and other related concepts, such as management units (MUs), Canadian designatable units (DUs), and adaptive evolutionary conservation has continued to be rigorous and brisk (Crandall et al. 2000; Fraser and Bernatchez 2001; Pearman 2001; Moritz 2002; Green 2005). However, distinct infraspecific populations of American vertebrates, except for salmonid fishes, can currently only receive legal protection as DPSs, not as ESUs.

A factor complicating the genetic study of desert tortoise populations has been human-mediated translocation. The tortoise has received much well-intended attention by governmental agencies and concerned citizens since the 1930s (California Code of Regulations 2007). Thousands of tortoises have been taken into captivity and then released. Still others have been translocated from one area to another in the desert. Commercial harvesting and interstate transportation have been significant.

Our objectives are to contribute to recovery efforts for this species by: 1) characterizing genetic differences in the Mojave populations to determine whether the existing 6 recovery units are genetically distinguishable and, if so, to what extent; 2) evaluating the potential effects of numerous releases and translocations of tortoises on genetic structure; and 3) placing the genetic data in the context of ecological and behavioral differences in desert tortoises to support the conservation of ecological and evolutionary processes.

METHODS

Sample Collection

We salvaged blood from desert tortoises used in research projects on health, disease, and physiology, and through collaboration with other scientists (Henen et al. 1997; Brown et al. 1999; Christopher et al. 1999, 2003; Edwards 2003). Desert tortoises were captured by hand in the field by following federal and state protocols (Averill-Murray 2000; Berry and Christopher 2001). Samples were collected from tortoises ($n = 628$) at 31 study sites that occur within the geographic range where the tortoise is federally listed (USFWS 1990) (Table 1; Fig. 1). We did not include sites from Nevada or the Beaver Dam Slope, Utah. Study sites were in remote areas as well as < 2 km from towns or human habitation. We also obtained mtDNA sequences from 4 *G. agassizii* from the Sonoran Desert of Arizona (Edwards et al. 2003), 1 sample of the bolson tortoise (*Gopherus flavomarginatus*) from a private collection, and 1 sample of the Texas tortoise (*Gopherus berlandieri*) from the Department of Animal Care and Technologies at Arizona State University, Tempe (J. Badman).

About 1 ml whole blood was collected via brachial, jugular, or subcarapacial venipuncture, and the samples were stored on ice or dry ice in (ethylenediamine tetraacetic acid [EDTA]), lithium heparin, or 95% ethanol. Most samples (from health and disease studies) were centrifuged first, the plasma was removed, and the red blood cells were retained and frozen for DNA extraction.

Molecular Techniques

Molecular procedures were conducted at the Genomic Analysis and Technology Core, University of Arizona. Genomic DNA was isolated from blood by overnight lysis with proteinase K at 55°C, followed by a phenol/chloroform extraction and isopropanol/sodium acetate precipitation (Goldberg et al. 2003). The DNA was resuspended in low TE (10 mM Tris-pH 8.0, 0.1 mM EDTA) and diluted to a 5 ng/μL working stock for polymerase chain reaction (PCR) amplifications.

MtDNA Sequencing. — We amplified an ca.1500–base-pair (bp) portion of the nicotinamide adenine dinucleotide dehydrogenase subunit (ND)3, arginine transfer RNA (tRNA) ND4L, and part of the ND4 genes by using primers Nap2 and New Gly (Arévalo et al. 1994; Britten et al. 1997; Edwards 2003). PCR followed Edwards (2003), and the PCR products were purified by using the QIAquick PCR purification kit (Qiagen, Valencia, CA) and were sequenced on an ABI Prism 3700 DNA Analyzer (PE Biosystems, Foster, CA). Internal primers were designed by using Oligo Primer Analysis Software 6.68 (Molecular Biology Insights, Inc, Cascade, CO): Nap2IN 5'AGGCGGTCAATAATGCTAATC3' and NewGIN 5'TAATAAAACCAGACAATGAAAAAC3'. These primers amplified an 1109-bp portion of ND3/ND4, which was aligned and evaluated by using Sequence Navigator 1.0.1 (Applied Biosystems, Inc, Foster, CA).

Nuclear DNA Assessment. — Data gathering was carried out on an ABI Prism 3730 DNA Analyzer (PE Biosystems). All samples were tested for 16 microsatellite loci (Table 2). The loci were PCR amplified in 6 separate multiplex reactions by using 5' fluorescently labeled forward primers. We sequenced selected products for all loci to verify repeat motifs. Repeat motifs were identified by using Sequence Navigator 1.0.1 (Applied Biosystems, Inc). Reliably scored, variable loci were used for analysis.

Analysis

Grouping of Samples. — Sample sizes from each of the 31 study sites ranged from 3 to 74 (Table 1). Study sites were assigned to 1 of 15 sample groups based on location, proximity to nearby sites (≤ 60 km), potential topographic or geographic barriers to movement of tortoises, region of the desert, recovery unit as described in the *Recovery Plan* (Fig. 1), and the need to maintain a minimum sample size for statistical analyses. Thus, the 15 sample groups contained 18–83 tortoises (Table 1). Sample group 11 combined individuals from Ivanpah, California ($n = 57$), which belong to the Northeastern Mojave Recovery Unit, with 3 tortoises from Shadow Valley in the Eastern Mojave Recovery Unit owing to close geographic proximity of the localities. We assigned groups to regions of the Mojave and Colorado deserts by using boundaries similar to those described in Rowlands et al. (1982), and the boundary between the Mojave and Colorado deserts as described in Jaeger (1957), Benson and Darrow (1981), Rowlands et al. (1982), and Turner et al. (1995). For boundaries delineating the northern and eastern regions within the Colorado Desert, we followed the *Recovery Plan* (USFWS 1994; Rowlands 1995a, 1995b).

MtDNA. — We selected 125 tortoises representing all recovery units, including 47 samples from the Northeast-

Table 1. Desert tortoise study sites and sample groupings representing 8 regions for the Mojave population.

Desert region/recovery unit	Study site	No. samples	Group	No. samples in group
Western Mojave	Desert Tortoise Research Natural Area	58	1	62
	Fremont-Valley	4	1	
	Hinkley	12	2	83
	Kramer	3	2	
	Edwards Air Force Base	57	2	
	Fremont-Kramer	11	2	
"Central Mojave"	Superior-Cronese	10	3	19
	Fort Irwin (Goldstone)	9	3	
	Fort Irwin (Tiefort)	31	4	31
	Fort Irwin (Soda Mtns.)	33	5	47
	Fort Irwin (Eastgate 2)	14	5	
"Southern Mojave"	Lucerne Valley	12	6	26
	Ord-Rodman	14	6	
	MCAGCC[a] (Emerson)	9	7	71
	MCAGCC (Sand Hill)	62	7	
	Daggett	74	8	74
	MCAGCC (Lavic Lake)	8	9	27
	MCAGCC (Maumee Mine)	7	9	
	MCAGCC (Sunshine Peak)	12	9	
	MCAGCC (Bullion)	16	10	19
	MCAGCC (Lava)	3	10	
Northeastern Mojave	Ivanpah	34	11	60
	Ivanpah (site 14)	23	11	
	Shadow Valley[b]	3	11	
Eastern Mojave	Fenner	4	12	31
	Goffs	27	12	
Northern Colorado	Chemhuevi	7	13	18
	Upper Ward Valley	11	13	
Eastern Colorado	Chuckwalla	18	14	37
	Chocolate Mtns.	19	14	
Upper Virgin River	near St. George, UT	23	15	23

[a] MCAGCC = Marine Corps Air Ground Combat Center.

[b] Population occurring in the Eastern Mojave Recovery Unit assigned to the Northeastern Mojave sample group for purposes of data analysis owing to geographic proximity.

Table 2. Observed microsatellite motifs in Mojave desert tortoises, *Gopherus agassizii*, compared with that of the originally described species or population.

Locus	Species originally described	Original repeat motif	Observed motif in Mojave population	Range of Mojave alleles	Range of Sonoran alleles
Edwards et al. 2003					
Goag3	*G. agassizii* (Sonoran)	$(CAA)_6$	$(CAA)_6$	6–7	6–9
Goag4	*G. agassizii* (Sonoran)	$(CAA)_{24}$	$CAA)_{24}$	12–32	7–30
Goag5	*G. agassizii* (Sonoran)	$(GAT)_8$	$GACGAA(GAT)_2GACGAA$	null	6–38
Goag6	*G. agassizii* (Sonoran)	$(TC)_8(AC)_{11}$	$(TC)_8(AC)_{11}$	17–-67	15–52
Goag7	*G. agassizii* (Sonoran)	$(AC)_3(GC)_5(AC)_{11}$	$(AC)_8(AT)_2GC(AC)_3(GC)_3(AC)_9$	13–28	12–28
Goag32	*G. agassizii* (Sonoran)	$(AC)_6$	$(AC)_6$	6	5–6
Schwartz et al. 2003					
GP26	*Gopherus polyphemus*	$(GT)_{12}$	$(GT)_7$	7	6–9
GP55	*G. polyphemus*	$(GT)_9$	$(GT)_7$	7–30	7–34
GP102	*G. polyphemus*	$(GT)_5(CT)_{13}(CA)_5$	$(TC)_2(TG)_2CG\ [(TG)_8(TC)_{14}]$[a]	19–42	19–36
GP15	*G. polyphemus*	$(GA)_{15}(GT)_8$	$(GA)_{14}(GT)_{20}$	13–52	13–56
GP19	*G. polyphemus*	$(GT)_9/(GT)_3(GA)_6$	Allele 1; $(GT)_3/(GT)_2GAAA(GA)_4$ Allele 2; $(GT)_7ATGTATGT/(GT)_2GAAA(GA)_5$	11 and 21	6, 11, and 21
GP30	*G. polyphemus*	$(GT)_{13}$	$(GT)_5(CT)(GT)_4$	10–17	5–29
GP81	*G. polyphemus*	$(GT)_{11}(GA)_{10}$	$(GT)_9GACA(GA)_8$	16–28	18–22
GP61	*G. polyphemus*	$(GT)_{12}$	$(GT)_4AT(GT)_6$ & $(GT)_{16}$	11–38	9–43
GP96	*G. polyphemus*	$(GA)_{11}$	$(GA)_7$	7	7
FitzSimmons et al. 1995					
Cm58	*Chelonia mydas*	$(CA)_{13}$	$(TA)_5(GA)_3GC(GT)_3$	12	12–13

[a] Complex repeat; unable to obtain entire sequence.

ern Recovery Unit, and sequenced their mtDNA for a total evidence analysis (Kluge 1989; Ernisse and Kluge 1993) of unique haplotypes only. Unweighted maximum parsimony analyses were performed on potentially informative characters by using PAUP* 4.0b10 (Swofford 2002). Most parsimonious trees were obtained by using the heuristic tree search algorithm with random addition of individuals, 10,000 replicates while retaining minimal trees only and holding 10 trees at each replicate, tree bisection-reconnection branch swapping with the steepest descent, and collapsed zero-length branches. All multistate characters were evaluated as nonadditive (unordered). Nodal consistency was assessed by using nonparametric bootstrap proportions (Felsenstein 1985) and decay analysis (Bremer 1994) performed in PAUP*. Relative nodal support was assessed by using bootstrapping with 10,000 random pseudoreplicates of the data, with each pseudoreplicate being replicated twice.

Bayesian inference was also used to hypothesize matriarchal history (Huelsenbeck and Ronquist 2001; Buckley et al. 2002; Nylander et al. 2004; Ronquist 2004). MrModeltest 2.2 (Nylander 2004) was used to select the best evolutionary model based on the Akaike Information Criterion (Akaike 1974, 1979). Hierarchical likelihood ratio tests (Goldman 1993) compared log-likelihood scores of 56 models. Bayesian inference, conducted by using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001), started with random trees. Six Markov chains were used, and the data set was run for 3×10^6 generations. Trees were sampled every 100 generations. Two independent analyses with different starting trees were run and the fluctuating values of likelihood were graphically monitored (Huelsenbeck and Bollback 2001). Log-likelihood scores of sample points were plotted against generation time to establish stationarity (Huelsenbeck and Ronquist 2001). The analysis was a priori required to achieve a split frequency standard deviation of ≤ 0.005. After discarding 25% of the sampled trees as burn-in, the remaining trees were used to generate a 50% majority rule consensus tree.

Nuclear DNA. — We used several methods of analyses to assess gene flow and population differentiation. Each of the methods had different assumptions and relied on different properties of the data, as noted below.

Population Structure. — We used 1) traditional techniques that a priori defined sample groups and 2) an a posteriori genotypic clustering method to analyze population structure. Individuals for which more than 3 loci did not amplify were discarded. Allelic frequency distributions for unique (study site or region restricted) and private alleles ($> 5\%$ in a sample group or region) were examined. Loci that exhibited more than 7 alleles were examined by using the log-likelihood-based (G-based) exact test (Goudet et al. 1996) in GENEPOP 3.1 (Raymond and Rousset 1995). A triangular contingency table and a modified version of the Markov-chain random walk algorithm (Guo and Thompson 1992) were used in ARLEQUIN 2.0 (Schneider et al. 2000) to detect significant departures from the Hardy-Weinberg equilibrium (H-W). The multiple tests were not Bonferroni corrected because we looked for trends only and not a precise application of statistical tests. The trends would have remained with a Bonferroni correction but the levels of significance (p-values) would have been raised, possibly to the extent of no significance. Default parameters in GENEPOP and ARLEQUIN were used for all Markov-chain tests and permutations.

Linkage equilibrium is assumed by some statistical tests and, thus, was necessary to confirm. GENEPOP tested for linkage disequilibrium (nonrandom association between loci) among all pairs of loci in the entire sample and within each group by using the method of Garnier-Gere and Dillmann (1992).

Population genetic structure was assessed under nonequilibrium conditions (Pearse and Crandall 2004; Manel et al. 2005). We used STRUCTURE 2.1 (Pritchard et al. 2000) to a priori define cohesive genetic units. Because it does not provide a good measure of genetic structuring in populations that exhibit nonlinear patterns of isolation-by-distance (IBD; Kimura and Weiss 1964; Pritchard et al. 2000), as do Mojave desert tortoises, STRUCTURE was used as a guideline only. An extension to the program by Falush et al. (2003) accounts for correlations between linked loci that arise in admixed populations. We evaluated the 15 sample groups (K populations) with 4 simulations of 500,000 iterations for each K by using the default parameters for an admixture model with a prior mean Φ_{ST} (F_{ST} sensu Weir and Cockerham 1984) of 0.06 (0.05 SD), based on the mean generated from our data set. (We initially also tried the analysis with a lower number of runs by using prior mean Φ_{ST} of 0.01, without a noticeable difference in the outcome.) The best model had the smallest value of K and the largest likelihood values.

To reduce the strongest effects of multilinear IBD, we performed an analysis on the Western Mojave Recovery Unit but first removed the northern- and southernmost samples. The analysis included sample groups 1–10 and used 1,000,000 iterations with a prior mean of Φ_{ST} at 0.01.

Population differentiation was also assessed by using WHICHRUN 4.1 (Banks and Eichert 2000), which calculates the likelihood of a given individual originating from either of 2 or more candidate populations. If the groups identified by STRUCTURE and/or the 6 units hypothesized in the Recovery Plan were distinct and not interconnected by frequent gene flow, then WHICHRUN should assign an individual to its source population with a high likelihood score and assign it to other populations with low scores. Stringency for population allocation used a selection criterion of the log of the odds ratio (LOD) for the 2 most likely source populations. The chance of error is equal to the inverse of this ratio; assignments with a LOD of at least 2 had a ≤ 0.01 chance of error.

Traditional equilibrium-based F-statistics, using analysis of molecular variance (AMOVA) in GENEPOP, were also employed to infer population structure. Inbreeding coefficients (Φ_{IS}; F_{IS} sensu Weir and Cockerham 1984) were calculated for each locus in each sample group. Genetic distances based on pairwise Φ_{ST} were calculated among groups and individuals by using GENEPOP and were visually assessed by producing a multidimensional monotonic scaling plot (MDS) that used the program NTSYS (Exeter Software, NTSYS pc 2.1, Setauket, NY). Goodness of fit was measured by using the Stress test (Kruskal and Wish 1978). Mantel tests obtained from NTSYS assessed correlations between genetic and geographic distances among sample groups. The Φ_{ST} values estimated population structure and gene flow by assuming mutation-drift or migration-drift equilibrium with symmetric migration in both directions for all pairwise combinations of populations. The Φ_{ST} values also assumed an island model that may not be met in desert tortoises, especially because they have experienced recent demographic declines (see Whitlock and McCauley 1999).

Demographic History. — Two very different models assessed historical changes in population density. First, BOTTLENECK (Piry et al. 1999) was used to test for evidence of historical changes in effective population sizes and deviations from equilibrium conditions for each of the sample groups, regions, and the entire population. Populations with recent reductions in effective population size should show an excess of heterozygosity (Cornuet and Luikart 1996; Spencer et al. 2000). Significance of the observed deviations, assuming the infinite alleles model, was determined by the Wilcoxon test as well as the Sign test method of Piry et al. (1999). Second, the M-ratio test of Garza and Williamson (2001) was used to investigate changes in population density and to evaluate bottlenecking, where M is the ratio of the total number of alleles (k) to the overall range in allele size (r). When rare alleles are lost during a population bottleneck, the number of allele size classes is reduced to a greater extent than the range in allele size. Value M is reduced in populations known to have declined in size. In total, 20 populations had the required number of individuals for applying this test. Bottlenecking was assumed to have occurred if M was above the critical value M_C (Garza and Williamson 2001). Congruent findings from the 2 tests would suggest that the results were not biased for any single method or set of assumptions.

Human-Mediated Translocations. — We compiled published and unpublished data and interviewed biologists in state and federal wildlife and land management agencies, then mapped localities of releases or escapes of captive tortoises and translocations of wild tortoises. The results of WHICHRUN assessed the source of an individual tortoise and assignments or misassignments to specific populations. BOTTLENECK, G-based exact tests in GENEPOP, and estimates of inbreeding values (Φ_{IS}) provided information on population trends. Significant deviations from H-W, estimates of recent gene flow and distributions of haplotypes from previously described analyses also provided valuable information.

RESULTS

MtDNA Evaluation. — Estimations of maternal history and population structure were based on *G. agassizii* from the Mojave population and the outgroup taxa (Table 3). All sequences were deposited in GenBank (Accession no. DQ649394–DQ649409).

Seven haplotypes were observed among the 125 *G. agassizii* from the Mojave population (Table 3). Five localities had a single haplotype, and 1 region, the Northeastern Mojave, had 3 sympatric haplotypes, likely a result of the greater extent of sampling at this locality. One haplotype, MOJ-A01, occurred in all but the Northeastern Recovery Unit. Similarly, haplotype MOJ-B01 was common in the Northeastern and Upper Virgin River recovery units but also occurred in low frequency in the Western Mojave and Eastern Colorado recovery units (Table 3). Haplotype MOJ-A02 occurred in 2 nearby localities in the Southern Mojave. MOJ-A03 was found in the nearby Western Mojave and Southern Mojave recovery units. In contrast, haplotypes MOJ-A04 and -B02 occurred at single locations only. Haplotypes within the Mojave population differed at most by 4–5 bp, or only 0.6%, and haplotypes MOJ-B01–03 differed from one another by 1–2 bp only, as did MOJ-A01–04.

Maternal History. — The phylogenetic evaluation was based upon 60 potentially cladistically informative nucleotide positions. In total, 842 nucleotide positions did not vary between the outgroup and ingroup taxa. Autapomorphies occurred at 22 nucleotide sites. The cladistic analysis of the sequences yielded 2 most parsimonious solutions (length = 77 steps, CI = 0.81, RI = 0.95, RC = 0.76). By using *G. flavomarginatus* as the primary outgroup, *G. berlandieri* was resolved as the sister group to all maternal lineages of *G. agassizii*. The consensus trees (Fig. 2) had 2 strongly supported lineages at the base of the tree, one containing Sonoran samples and the other containing samples from the Mojave population. Within the Mojave population, 2 major sublineages were resolved: Haplogroup A, "broadly distributed," and Haplogroup B, Northeastern Mojave. Both lineages contained 1 haplotype that was relatively broadly distributed (Table 3), along with alternative haplotypes. The 2 most basal nodes for *G. agassizii* were strongly supported having bootstrap proportions of 100% and decay indices of 9–10 steps for the Sonoran and Mojave lineages, respectively (Fig. 2). Within the Mojave, Haploclades A and B were only weakly supported; bootstrap proportions = 53%–65% and decay values were 1–2 steps.

When using MrModeltest, the general time reversal plus invariant sites (GTR + G) model was selected for use in the Bayesian inference analysis (–lnL = 2111.7654; K = 9; AIC = 4241.5308). Bayesian inference resulted in

Table 3. The distribution of mitochondrial deoxyribonucleic acid haplotypes from the Mojave desert tortoise, *Gopherus agassizii*.

Desert region/ recovery unit[a]	Group	Haplogroup A				Haplogroup B			Total
		MOJ-A01	MOJ-A02	MOJ-A03	MOJ-A04	MOJ-B01	MOJ-B02	MOJ-B03	
Western Mojave	1	2				1			3
	2	10		1					11
Central Mojave	3	6							6
	5	2							2
Southern Mojave	6	6	2						8
	7	7		1					8
	8	3							3
	9	5	1						6
	10	6							6
Northeastern Mojave	11					40	1	6	47
Eastern Mojave	12	8							8
Northern Colorado	13	3			1				4
Eastern Colorado	14	6				1			7
Upper Virgin River	15	1				4		1	6
Total		65	3	2	1	46	1	7	125

[a] Within the Mojave Desert, 2 major sublineages were resolved: Haplogroup A "broadly distributed", and Haplogroup B, Northeastern Mojave (Fig. 2). The greater relative sampling in the Northeastern Mojave (group 11) reflected an attempt to locate a haplotype from Haplogroup A.

a tree that was identical to the maximum parsimony consensus trees. The Bayesian posterior probabilities were higher than the bootstrap proportions (Fig. 2).

Microsatellite Evaluation. — Of the 16 loci surveyed in 628 desert tortoises (Table 1), 11 were highly variable and informative: Goag03, Goag04, Goag06, Goag07, GP15, GP19, GP30, GP55, GP61, GP81, and GP102. Five loci showed insufficient variation and were excluded from our analyses: GP26, GP96, Cm58, Goag05, and Goag32. For locus Goag03, only 2 study sites exhibited variation: groups 11 and 15 (Northeastern Mojave and the Upper Virgin River recovery units, respectively). For all microsatellite loci used in this study, individual genotypes were summarized by regional groups and are available from the Internet home page of RWM (www.zoo.utoronto.ca/drbob/publications).

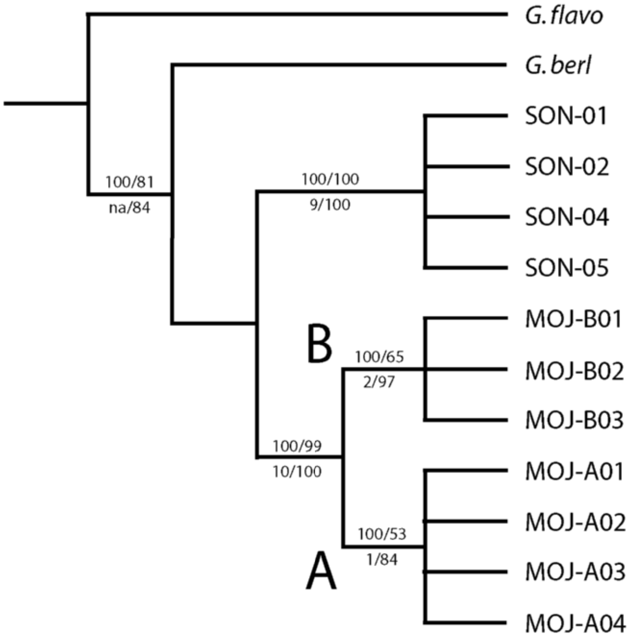

Figure 2. A 50% majority rule consensus tree based on maximum parsimony and Bayesian inference evaluations of the mitochondrial deoxyribonucleic acid sequence data from tortoises, genus *Gopherus*. SON = Sonoran and MOJ = Mojave populations of the desert tortoise (*Gopherus agassizii*) and outgroups G. berl (*G. berlandieri*) and G. flav (*G. flavomarginatus*). Numbers above the branches are given as frequency of resolution in the maximum parsimony evaluation/bootstrap proportions, and below as Bremer support/Bayesian posterior probabilities. Na = not applicable, and letters at nodes denote haplogroup lineages of Mojave populations discussed in text.

Major differences occurred between repeat motifs at some microsatellite loci in *G. agassizii* when compared with species or the population for which the locus was originally isolated, including GP19, GP30, GP61, GP81, and GP102 (Table 2). We were not able to precisely determine the motif for GP102 in *G. agassizii*. Homozygous amplicons were vague in the middle of the sequences, suggesting that 2 alleles were present. Fragment analysis did not allow determination of a heterozygous state (difference in repeat motifs) when amplicon lengths were equal. We did not clone these products to determine the competing sequences but rather made an arbitrary assignment of repeat numbers. Consequently, data for GP102 were not necessarily reflective of all possible heterozygous states.

Locus GP61 exhibited 2 different motif states; alleles having more than 16 repeats had a simple dinucleotide motif, $(GT)_{16+}$. However, alleles scoring in the range of 10–12 repeats had a compound motif, $(GT)_4AT(GT)_6$. As in the Sonoran population (Edwards et al. 2004), heterozygous individuals had both motifs. The simple motif had a greater range of allelic states than the compound motif.

Schwartz et al. (2003) originally described the compound motif for GP19 in *Gopherus polyphemus* as $(GT)_9/(GT)_3(GA)_6$. We found a dramatically derived state

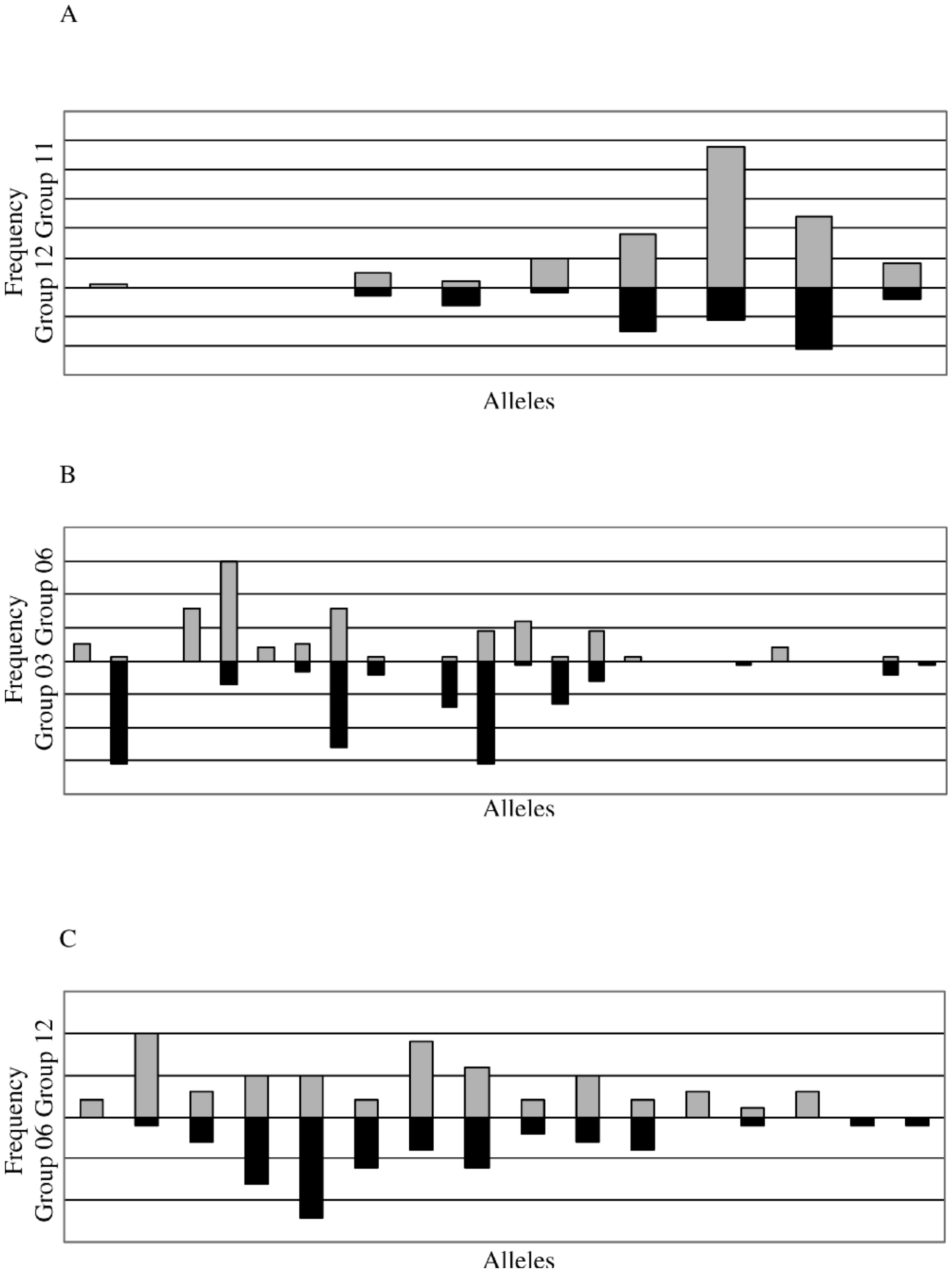

Figure 3. Comparison of allelic frequencies between sample groups of desert tortoises, *Gopherus agassizii*, from the Mojave population by using the G-based exact test for genotypic differentiation. Sample groups refer to Table 1. A: Locus GP81, $p = 0.024$, SE $= 0.002$; B: Locus GP102, $p < 0.001$, SE < 0.001; C: Locus Goag04, $p = 0.031$, SE $= 0.003$.

in our Mojave samples of *G. agassizii*, such that allele 11 sequenced as $(GT)_3/(GT)_2GAAA(GA)_4$ and allele 21 sequenced as $(GT)_7ATGTATGT/(GT)_2GAAA(GA)_5$. Consequently, we could not use analyses that required a stepwise mutation model, such as R_{ST} (Slatkin 1995).

Some dinucleotide loci exhibited imprecise pherograms (e.g., stutter peaks) when the number of repeats exceeded 25. A score of "35" could not be differentiated from "34" or "36". Consequently, pherograms were scored by using a standardized rule set for consistency with error on the conservative side. Loci GP15, GP61, GP102, and Goag06 may have reached the upper limits of our ability to detect repeat numbers, because larger amplicons had very low intensity pherograms. Generally, alleles with more than 55 repeats were not scored, and, thus, we likely missed some alternative alleles.

The distributions of allele size classes for most loci were not normally distributed. Some were highly skewed, and others exhibited multiple peaks (Fig. 3). Unique and private alleles were detected in several sample groups at some of the more variable loci. In some cases, private alleles comprised a high proportion of the alleles observed within a population. For example, sample group 14 had 4 alleles at GP30; the private allele composed 25% of all alleles (Table 4) but it occurred at a frequency of < 5%.

Table 4. Distribution of unique and private alleles in 15 sample groups (summarized in Table 1) of desert tortoises from the Mojave population.[a]

Sample	GP61			GP19			GP102			GP30			GP55			GP15			GP81			Goag4			Goag06			Goag7			Goag3		
group	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%	T	U	%
1	14			2			7			9	1	11	9			17			7	2	29	16			26			5			1		
2	15			2			14			8	1	13	8	1	13	24	1(1)	4.2	5			17	1	5.9	22			4			1		
3	9			2			9			5			8	1	13	15			5			13			16			4			1		
4	11			2			11			7			11			14			6			12			19			4			1		
5	13			2			11			7	1	14	12	1	8.3	16			5			15			21			5			1		
6	10			2			10			4			6			9			6			13			18			4			1		
7	16			2			13	1	7.7	8	2	25	7			21			7			12			21			4			1		
8	14			2			15			7			11			20	1	5	7	1	14	11			33			5			1		
9	11			2			12			6	1	17	7	1(1)	14	10			7			12			22			5			1		
10	13			2			7	1(1)	14.3	4			7			14	1	7.1	7			9			14			4			1		
11	15			2			16	1	6.3	8			6			19			8	1	13	16			19			6			2		
12	18			2			12			9			7			15			7			14			15	1	6.7	4			1		
13	13	1	7.7	2			12			10	2(1)	20	5			14			7			11	1	9.1	14			5			1		
14	15	1(1)	6.7	2			12	1(1)	8.3	4	1	25	9			13			6			11	1(1)	9.1	21			5			1		
15	11			1			12	1(1)	8.3	7			3			15			5			10			15			3			2		
Total	27			2			24			21			17			37			11			22			49			5			2		

[a] T = total number of allelic states observed in a sample group; U = number of alleles unique to the sample group; parenthetic values are the number of unique alleles that occur at a frequency > 5% (private alleles) in a sample group relative to the total number of alleles; % = the percentage of alleles that are unique in a sample group [(U/T) × 100]. No private alleles in a population occurred at a frequency > 8%.

The frequency of occurrence for the relatively rare, private allele was always ≤ 8%.

Most sample group pairwise comparisons between distributions of allelic frequencies (Fig. 3) were found to be significantly different by the G-based Exact test (Goudet et al. 1996). Three sample groups deviated from H-W in exhibiting a greater number of heterozygotes than expected (Table 5). By using a 5% cutoff, about 1 deviation is expected for each locus, except for Goag3. Three loci showed excessive deviations from expectations in the form of heterozygote deficiencies: GP30, G81, and Goag06. In total, 24.5% of the data points showed deviations from H-W, with 8.6% owing to Goag06 alone (Table 5).

Garnier-Gere's and Dillmann's (1992) test rejected the null hypothesis for linkage disequilibrium (equilibrium for locus pairs) for 45 (of 165) locus pairs within 15 sample groups. Nine sample groups had a percentage of total pairwise comparisons with p-values > 0.05 (range 0.0%–26.7%). However, locus pairs did not consistently exhibit disequilibrium among groups.

Bayesian likelihood values for all runs by using STRUCTURE typically stabilized after 50,000–100,000 iterations after burn-in. The analyses obtained the lowest average Ln for 6 subpopulations (Table 6). These subpopulations were concordant with the recommendations in the *Recovery Plan*. Because substantial differentiation was observed in the Western Mojave Recovery Unit, as revealed by Φ_{ST} values, we removed populations 11–15 and performed a new analysis to reduce the affects of IBD. This analysis suggested that the current Western Mojave Recovery Unit supported 4 subpopulations (Table 6): sample groups 1–2, 3–5, 8, and 6–7 plus 9–10 (Fig. 4).

A 2-dimensional, monotonic MDS plot displayed population differentiation among sample groups (Fig. 5). It had a stress of 1.39, a fair to good fit by Kruskal's and Wish's (1978) index. The 15 sample groups clustered complementary to their geographic proximities, as anticipated when assuming gene flow. Geographically distant sample groups 11 and 15 were noticeably separated from the other groups.

Population assignment tests correctly placed the majority of individuals back to their sample groups with high stringency (Table 7). Individuals not assigned to a sample group were frequently assigned to a geographically nearby group or to one within the same region. Geographically proximate groups 12 and 13 occurred near the boundary of 2 desert regions, the eastern Mojave Desert and northern Colorado Desert (Fig. 1). The population assignment evaluations had difficulty distinguishing individuals between these 2 recovery units. Whereas, 80% of the samples from group 11 were correctly assigned, only 48% of 31 samples from group 12 were correctly assigned. However, 87% of tortoises from group 12 were correctly assigned to groups 12 and 13 combined, indicating that, in this case, geographic proximity was a better predictor of genetic structuring

Table 5. Summary of deviation from Hardy-Weinberg expectations for 11 variable microsatellite loci and 15 sample groups of the desert tortoise, *Gopherus agassizii.* Sample groups refer to Table 1.

Locus	No. comparisons	No. heterozygote excess	No. heterozygote deficiency	Range in no. of repeats
GP61	15	0	2	11–38
GP19	14	0	0	11–21
GP102	15	1	1	19–42
GP30	15	0	7	10–17
GP55	15	0	3	7–30
GP15	15	0	2	13–52
GP81	15	0	6	16–28
Goag4	15	1	0	12–32
Goag06	15	0	13	17–67
Goag7	15	1	0	13–28
Goag3	2	0	0	6–7

than recovery unit. A similar trend was discovered for tortoises in group 13.

When sample groups were combined to reflect current recovery units, and when sample groups 12 and 13 were combined, assignment scores of $\geq$ 80% were obtained (Table 7). For the Western Mojave Recovery Unit, we deleted geographically distant sample groups (1, 2, 11–15) and re(-)ran the assignment test. We combined samples 3–5 and samples 6–10, because they had higher proportions of misassigned individuals than all other units (Table 7). Although not given in Table 7, the percentage of individuals correctly assigned to the proposed Central Mojave (samples 3–5) and Southern Mojave (samples 6–10) recovery units combined was 52% each, with 24% being assigned to the combined unit as the second most likely assignment and 13% assigned to the adjacent Western Mojave Recovery Unit.

Finally, we combined the sample groups to reflect geographic regions, which reflected the current recovery units (Table 7). This treatment recognized variation within the Western Mojave Recovery Unit. In total, 8 regions were identified. Assignment scores ranged from 59.6% to 95.7%. The more fine-grained analyses, those that included a greater number of subdivisions, yielded lower assignment scores.

Geographic substructuring was further assessed by breaking and recombining specific units. The assignment tests produced 96%–98% accuracy when the distribution of tortoises was divided into 2 groups: Northeast (11, 15) and Central (1–10, 12–14), respectively. When geographically proximate groups were split and recombined, the assignment tests invariably decreased, some to less than 50% (sample groups 2, 6, and 8).

The hierarchical analysis of molecular variance indicated the absence of panmixia; significant genetic structuring was discovered. The AMOVA revealed that 93.9% ($p < 0.001$) of the observed variation was partitioned among individuals within sample groups ($\Phi_{IT} = 0.939$), whereas only 6.1% of the variation was among the sample groups ($\Phi_{ST} = 0.061$, $p < 0.001$). The positive significant correlations between genetic distance (pairwise Φ_{ST}) and geographic distance accounted for approximately 65% of the observed variation (Mantel test; $r^2 = 0.646$, $p = 0.002$).

By using BOTTLENECK, we detected a significant excess in heterozygosity in 2 sample groups, 11 and 15, the Northeastern Mojave and Upper Virgin River recovery units. The Wilcoxon Test with the (infinite alleles model [IAM]) detected an excess in both groups but the Sign Test (IAM) method of Piry et al. (1999) identified group 15 only. No deficit or excess in heterozygosity was detected when the data for all groups were combined. All sample sets fit the expected beta distribution (Cornuet and Luikart 1996), thus providing no evidence for bottlenecking. By using the method of Garza and Williamson (2001) to detect potential reduction in population size, all values of M fell above the critical value M_C. However, the results may not be reliable, because this test assumed stepwise mutation.

Human-Mediated Translocations. — Native Americans undoubtedly moved desert tortoises from one place to another (as implied in Schneider and Everson 1989). The distances were probably limited, except for annual gatherings for mourning ceremonies (i.e., Las Vegas Band, Southern Paiute: Kelly, no date) and the result may have been death for the tortoises.

Throughout the 20th century, tortoises were captured for domestic pets and were translocated for various purposes. Captive tortoises currently or formerly kept by residents of desert communities often escape or are deliberately released into adjacent desert lands. The sources of the captives may or may not be local relative to the point of escape or release. Escaped captives are so common that a publication gives actions to take when a former captive is found (Berry and Duck, 2006). Captives have been observed wandering within city limits or nearby in Ridgecrest, Barstow, Ft. Irwin, Victorville, and Twentynine Palms in the Western Mojave Recovery Unit; Needles in the Eastern Mojave Recovery Unit; Las Vegas in the Northeastern Mojave Recovery Unit; and St. George in the Upper Virgin River Recovery Unit. Tortoises are often taken to or released at protected areas such as parks and Natural Areas (Howland 1989; Ginn 1990; Jennings 1991; Connor and Kaur 2004).

Thousands of tortoises were released in the southwestern deserts by humane societies, California Department of Fish and Game, Nevada Department of Wildlife Resources, Utah Division of Wildlife Resources, State and National Park personnel, academicians and others (Fig. 6). Data are limited before the 1960s, but releases were documented for California and Utah (Hardy 1945; Woodbury and Hardy 1948; Jaeger 1950, 1955). Woodbury and Hardy (1948) surveyed Beaver Dam Slope, Utah (Northeastern Mojave Recovery Unit) for tortoises between 1936 and 1946. At least 6.1% of 281 tortoises found showed signs of previous captivity. Releases also occurred in the

Table 6. Inferred population structure obtained from the software program STRUCTURE 2.1 for all samples, and for a subset of samples from the current Western Mojave Recovery Unit (sample groups 1–10).[a]

All samples (n = 628)

	Ln (variance below)				
K	Run 1	Run 2	Run 3	Run 4	Average Ln
1	–25,140.5	–25,144.0	–25,143.6	–25,143.3	–25,142.9
	99.7	106.1	106	105.8	
2	–24,362.2	–24,360.6	–24,360.8	–24,361.2	–24,361.2
	463.9	460.7	462.6	463.3	
3	–23,644.7	–23,646.2	–23,647.9	–23,648.6	–23,646.9
	568.4	570.5	572.8	574.9	
4	–23,283.3	–23,275.4	–23,269.5	–23,272.6	–23,275.2
	827.5	810.6	800.5	804.8	
5	–23,134.7	–23,038.1	–23,030.7	–23,042.5	–23,061.5
	1049.5	1056.0	1041.2	1062.6	
6	–22,881.4	–22,886.7	–22,883.4	–22,893.2	–22,886.2
	1249.2	1260.3	1251.2	1275.1	
7	–23,042.2	–22,840.3	–24,213.8	–24,745.5	–23,710.5
	1921.8	1521.7	4220.5	5220.9	
8	–22,901.4	–23,454.5	–23,144.8	–22,964.3	–23,116.3
	1712.3	3043.6	2204.3	1858.5	
9	–23,538.9	–24,007.6	–22,951.0	–23,041.1	–23,384.7
	3494.4	4412.3	2335.7	2230.9	
10	–22,857.7	–24,696.7	–22,900.7	–22,900.7	–23,339.0
	2208.1	5872.7	2262.5	2280.9	
11	–23,305.8	–24,272.3	–24,176.7	–24,377.2	–24,033.0
	3318.1	5406.3	5027.1	5490.7	
12	–23,236.8	–24,848.4	–23,590.5	–34,317.7	–26,498.4
	3426.8	6666.9	4129.0	25,502.9	
13	–24,346.5	–23,339.1	–34,657.2	–28,975.2	–27,829.5
	5879.4	3820.1	26,339.3	15,064.1	
14	–31,546.3	–560,553.8	–31,303.2	–24,971.2	–162,093.6
	20,362.5	1,077,674.6	19,809.4	7242.0	
15	–133,340.8	–28,256.8	–27,197.9	–41,616.9	–57,603.1
	223,973.3	13,936.0	11,869.1	40,664.7	

Western Mojave samples (n = 459)

K	Run 1	Run 2	Run 3	Run 4	Average Ln
1	–17,343.6	–17,342.7	–17,338.4	–17,339.0	–17,340.9
	99.8	97.2	90.7	90.8	
2	–16,870.6	–16,871.0	–16,870.0	–16,873.2	–16,871.2
	405.0	406.7	405.5	411.5	
3	–16,968.7	–16,715.6	–16,722.3	–16,626.4	–16,758.3
	1218.3	693.6	847.8	657.2	
4	–16,438.7	–16,434.3	–16,432.9	–16,438.4	–16,436.1
	874.5	863.0	860.4	871.3	
5	–16,380.9	–16,404.5	–16,419.0	–18,206.9	–16,852.8
	1068.9	1114.4	1143.6	4629.7	
6	–16,742.5	–16,392.3	–16,418.5	–17,106.1	–16,664.9
	1876.6	1163.9	1217.5	2750.5	
7	–16,778.8	–17,811.3	–16,450.6	–18,021.6	–17,265.6
	2430.1	4440.4	1540.5	4871.7	
8	–16,343.7	–18,314.1	–18,520.9	–16,417.4	–17,399.0
	1837.0	5698.8	5924.8	1746.6	
9	–20,559.6	–17,456.7	–16,346.8	–19,067.6	–18,357.7
	10,289.0	4207.3	1842.1	7354.0	
10	–18,184.4	–406,665.0	–19,777.8	–21,971.6	–116,649.7
	5770.3	780,420.0	8955.7	13,321.4	

[a] K = the number of populations set as the a priori for the simulation; Ln = the log likelihood of the data averaged over all iterations after burn-in (with variance reported below); and the average Ln for all 4 runs for a given simulation. (For all simulations: 250,000 iterations per run with a burn-in of 5000).

vicinity of St. George and the Upper Virgin River Recovery Unit (Hardy 1945).

From the late 1960s to the mid 1970s, the California Department of Fish and Game sponsored numerous captive releases and kept records for > 800 individuals (Fig. 6). Their last official release was the rehabilitation experiment at the Quarterway and Halfway Houses in the Living Desert Reserve and Ft. Soda, respectively, in the late 1970s. Among 200 tortoises initially in the program, 30 survived, only to be moved to private lands in the Antelope Valley (Cook et al. 1978; Weber et al. 1979; Cook 1983).

In Nevada, the first documented releases of captive tortoises occurred on the Desert Game Range in 1973 (B.L. Burge, *pers. comm.*, December 2005; Fig. 6). In the late 1970s and early 1980s, employees of the Nevada

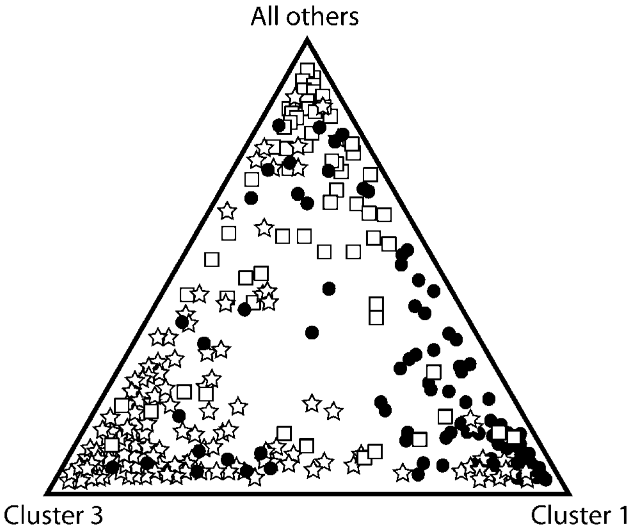

Figure 4. Triangle plot of the estimated membership coefficients for each individual in the Western Mojave Recovery Unit. Symbols correspond to sampling groups (given in Table 1) when the number of populations (K) is K = 3: circles = sample groups 1 and 2, squares = sample groups 3–5, stars = sample groups 6–10. Note the general clustering in the corners of each group and the overall pattern of admixture (gene flow). The cluster of stars in the circle samples depicts individuals mostly from Group 8, which is geographically the most proximate to the circle sample group.

Department of Wildlife Resources released hundreds of captive tortoises onto desert lands (R.J. Turner, *pers. comm.*, December 2005).

State and federal agencies approved the release of numerous captive and wild tortoises in 1997 at a long-term release site in southern Nevada (Field 1999). Additional translocation projects occurred throughout Nevada between 1990 and 2005 (Corn 1991; Nussear 2004; Charles Le Bar, *pers. comm.*, December 2005).

Between 1973 and 1983, the Utah Division of Wildlife Resources released at least 195 captive tortoises on Beaver Dam Slope (Coffeen, *pers. comm.*, December 2005; Coffeen 1984, 1985). In 1980, a general survey conducted throughout 324 km^2 of the area revealed that 21.9% of 105 located tortoises were marked captives (Minden 1980). Tortoises were also released on the historical Woodbury and Hardy (1948) site; when the study site was surveyed in 1981, 23.3% of the 73 tortoises observed were marked captives (Minden and Keller 1981). In the mid to late 1980s, captive tortoises were released in the Upper Virgin River Recovery Unit at Grapevine Pass and Red Cliffs Recreation Area (Coffeen 1986); 71 captive tortoises were also released at Hurricane Cinder Knolls (McLuckie, unpubl. data, 2006).

Evidence exists of a substantial transfer of tortoises from the western Mojave Desert in California to Utah. In April of 1970, 2 wardens arrested a commercial collector who claimed to have taken thousands of tortoises from the Western Mojave Recovery Unit of California between the 1960s and April 1970 and sold them commercially in Salt Lake City, Utah (Berry 1984). Some of these tortoises may have been released on the Beaver Dam Slope and north of St. George in the 1970s and early 1980s in what are now the Northeastern Mojave and Upper Virgin River recovery units.

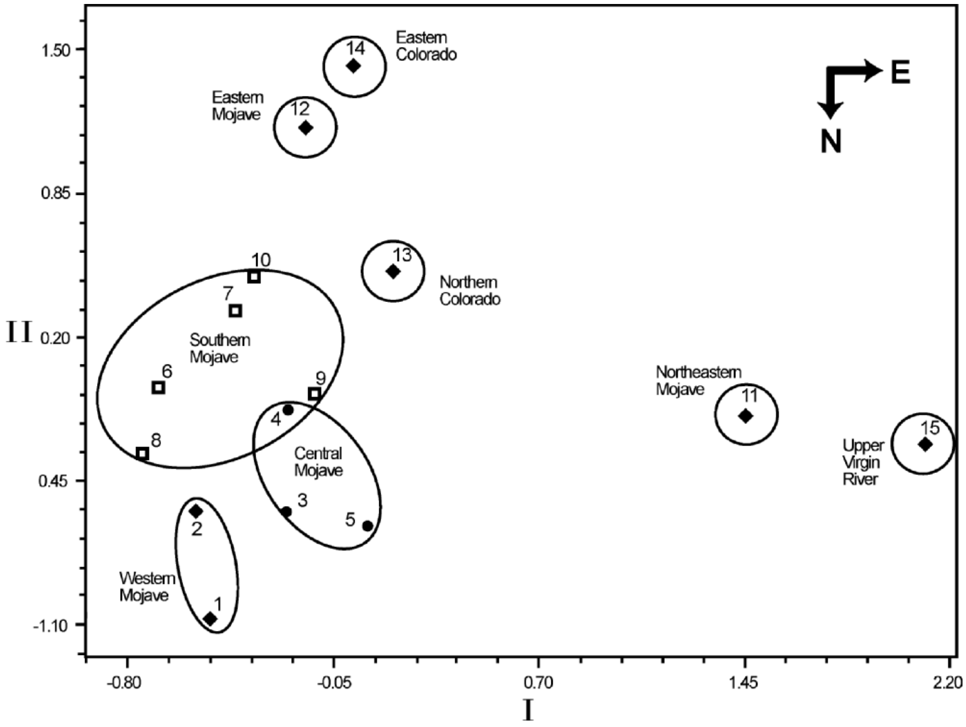

Figure 5. A 2-dimensional scaling plot of genetic distances (Φ_{ST}) for 15 sample groups of desert tortoises, *Gopherus agassizii*, from the Mojave population. Open squares and solid circles indicate samples from the southern and central Mojave Deserts, respectively.

Table 7. Population assignment tests for desert tortoises from the Mojave population and 8 desert regions or recovery units. The initial evaluation treated all 15 sample groups separately. The second treatment combined tortoises into units reflecting the recovery units recommended in the 1994 *Recovery Plan* except for combining sample groups 12 and 13. The third treatment considered populations on the basis of existing and proposed recovery units.

Sample group	No. samples	No. correctly assigned	% Correctly assigned	% With LOD > 2[a]	No. assigned to same region or neighboring group	% Assigned to same region
1	62	42	67.7	58.1	8	80.6
2	83	26	31.3	19.3	16	50.6
3	19	10	52.6	47.4	3	68.4
4	31	11	35.5	22.6	11	71.0
5	47	25	53.2	51.1	12	78.7
6	26	12	46.2	42.3	11	88.5
7	71	20	28.2	19.7	37	80.3
8	74	34	45.9	35.1	13	63.5
9	27	8	29.6	14.8	14	81.5
10	19	10	52.6	52.6	5	78.9
11	60	48	80.0	78.3	0	80.0
12	31	15	48.4	38.7	12 (to group 13)	87.1
13	18	10	55.6	27.8	3 (to group 12)	72.2
14	37	28	75.7	59.5	0	75.7
15	23	22	95.7	91.3	0	95.7
Combined groups						
15	23	23	100			
11	60	51	83.3	10		
12, 13	49	41	81.6	8.2		
14	37	35	91.9	5.4		
1–10	459	377	80	8.5		
Region						
Western Mojave	164	139	84.8			
Central Mojave	97	66	68.0			
Southern Mojave	198	118	59.6			
Northeastern Mojave	60	49	81.7			
Eastern Mojave	31	17	54.8			
Northern Colorado	18	13	72.2			
Eastern Colorado	37	33	89.2			
Upper Virgin River	23	22	95.7			

[a] LOD = log of the odds ratio.

DISCUSSION

Maternal History. — Two distinctive maternal lineages exist, one associated with the Sonoran population in Arizona and the other with the Mojave population. By using *G. flavomarginatus* as the outgroup, the sister group to *G. agassizii* was *G. berlandieri* (Fig. 2). This resolution differed from that of Lamb et al. (1989). Rooting with the same outgroup, they found that the Sonoran *G. agassizii* was the sister group of *G. berlandieri* and exclusive of the Mojave population. The difference could have resulted from several factors. Lamb et al. (1989) evaluated restriction fragment length polymorphisms, and we used more precise sequences. They also had greater taxonomic and geographic sampling. Although we might have reached a similar conclusion if we had used the same coverage, this was unlikely. The difference likely resulted from their use of presence/absence coding of nonhomologous fragment lengths.

Within Mojave population samples, little differentiation occurred among the 7 haplotypes (Fig. 2). Two primary maternal sublineages occur in the Mojave population, but the minor level of differentiation was not indicative of taxonomic differentiation. In contrast, the substantial sequence differentiation between Mojave and Sonoran (Arizona) populations is consistent with the hypothesis that *G. agassizii* consists of more than one species (Berry et al. 2002).

Descriptive Statistics of Microsatellite nuclear DNA (nDNA). — The motif differences in interspecies amplification of microsatellite loci indicated that evaluation of data required species-specific and even population-specific sequence information. Loci amplified between species (and within species too; Estoup et al. 2002.) did not necessarily follow assumptions of the stepwise mutation model.

Deviations from H-W could have several sources. Excess of homozygotes at some loci (e.g., Goag06) could have resulted from nonamplifying alleles, as a consequence of motif anomalies. Translocations of tortoises throughout the Mojave population also might have contributed to the excess of heterozygosity. For cases of heterozygotic deficit, ambiguities associated with high numbers of repeats might have artificially inflated the number of observed homozygotes or elevated Φ_{IS} values if translocated tortoises had very different allele frequencies

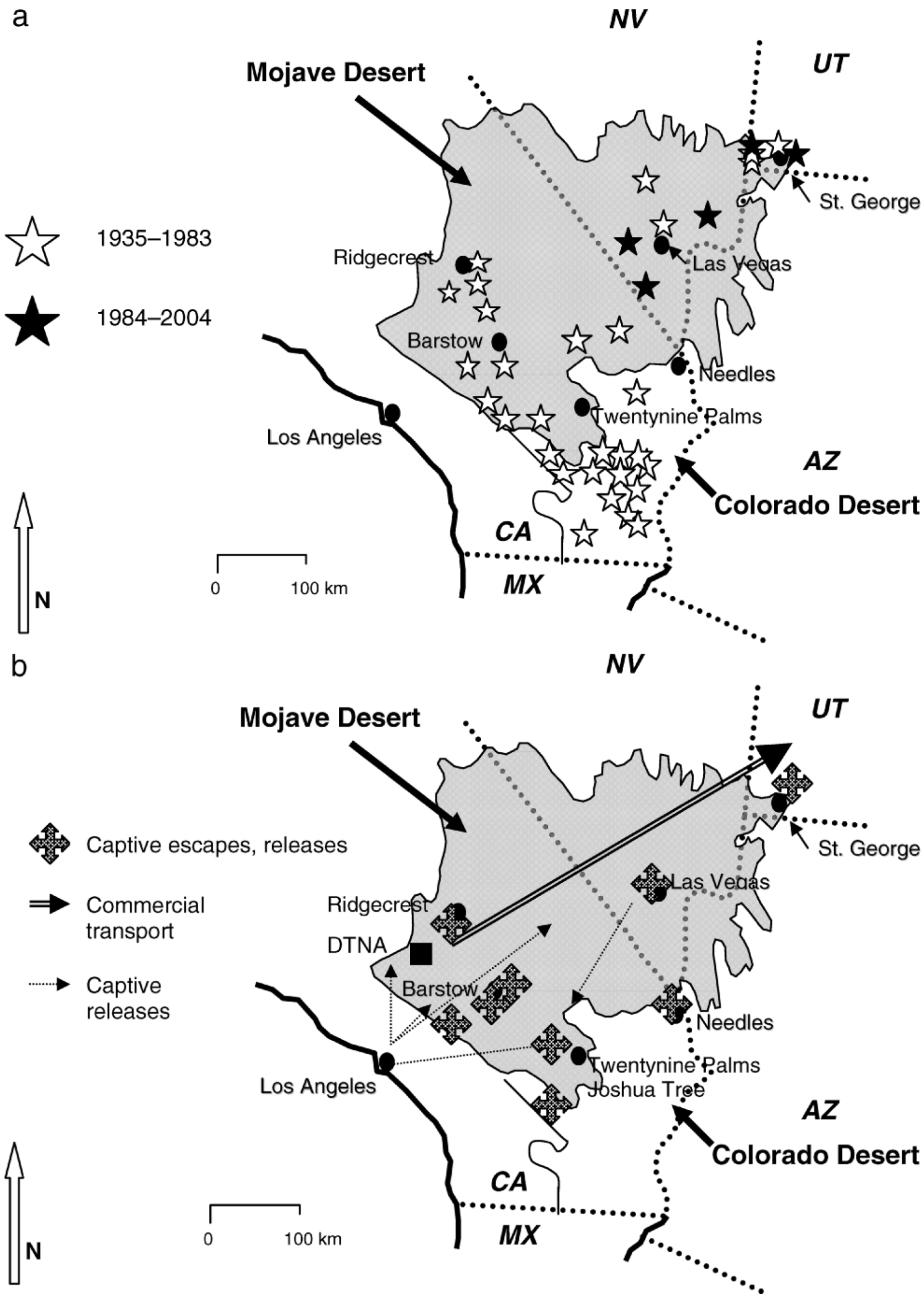

Figure 6. (a) Locations of captive desert tortoises, *Gopherus agassizii*, released by the California Department of Fish and Game, Nevada Department of Wildlife, Utah Division of Wildlife Resources or by others, as described in government reports and university theses and dissertations. The shaded area indicates the limit of the Mojave Desert. (b) Locations of areas where captives escaped or were released outside of desert towns. Tortoises were taken from the Los Angeles basin and released at places such as the Desert Tortoise Research Natural Area (DTNA) or Joshua Tree National Park. There were also large-scale commercial transfers of tortoises.

(a Wahlund effect, lower than expected heterozygosity owing to population substructuring). Technical difficulties of accurately scoring heterozygotes with high numbers of repeats surely contributed to the estimates of heterozygosity deficiencies at Goag06 and possibly at other loci (Table 5). Unfortunately, the proportions of misscored loci cannot be accurately partitioned from the data set to examine for a Wahlund effect (e.g., Chapuis and Estoup 2007).

In total, 24.5% of the data points showed deviations from H-W in the form of heterozygote deficiencies (Table 5). Such deviations may not significantly affect our conclusions. Dankin and Avise (2004) showed that 20% of the data points can deviate from H-W, without affecting the accurate determination of parentage. Empirically, the great correspondence between the results of the microsatellite analyses and ecological boundaries supports our assumption of the utility of the data irrespective of their deviations from H-W expectations.

For tortoises, IBD (isolation-by-distance) affected the probability of individuals mating with one another and violated the assumption of panmixia for statistical tests. Significant pairwise associations of some loci (Table 5) may have reflected an absence of panmixia (i.e., a Wahlund effect), mating systems or problems in resolving alleles. However, because significant linkage disequilibrium was not observed in all groupings, this explanation was unlikely. The greater than expected deviations from H-W were strongly paralleled by Φ_{IS} values. Some deviations from H-W owed to technical constraints (e.g., Goag06), but this was unlikely for other loci (e.g., GP30, GP81). Some positive inbreeding coefficients and departures from H-W may have been because of population structure. However, inbreeding was unlikely to have occurred because most loci did not have significant Φ_{IS} values within a sample group.

Gene Flow. — Genetic structuring was strongly associated with geography (Slatkin and Maddison 1990), IBD, and the limited dispersion of individual tortoises (Mantel test; $r^2 = 0.646$, $p = 0.002$). The results of the AMOVA indicated the absence of panmixia. IBD was also reported by Britten et al. (1997) for allozyme and mtDNA data, and by Edwards et al. (2004) for Sonoran tortoises. Microsatellite variability was greater within than among sample groups, suggesting that the Mojave metapopulation was relatively homogeneous, i.e., the common alleles were broadly distributed. Gene flow likely occurred throughout populations in California, at least until the recent proliferation of anthropogenic barriers. The distribution of low-frequency, unique microsatellite alleles supported the hypothesis that the genetic structure resulted from gene flow and not common ancestry. Indeed, Edwards et al. (2004) noted that desert tortoises were ideal organisms for applying the IBD model, because they are distributed across the landscape in patches, and the difficulty of dispersion is a function of geography.

Bottlenecking. — The excess of heterozygosity in samples from the Northeastern Mojave and Upper Virgin River recovery units could have resulted from recent bottlenecking. However, this possibility was not supported by the ratio of the total number of alleles to the overall range in allele size. Population declines in the Northeastern Mojave and Upper Virgin River recovery units have been well documented in recent years (USFWS 1980; Minden and Keller 1981; Fridell and Coffeen 1993; McLuckie et al. 2004). Although other regions also experienced population declines (Berry and Medica 1995; Brown et al. 1999; Christopher et al. 2003), they did not show genetic evidence of bottlenecks. This inconsistency may have been because of at least 4 factors. First, our samples were collected over 10 years and this could have precluded the effects of recent declines. Second, the time frame for sampling may have been too short for observing a shift in heterozygosity for a long-lived species with a long generation time. Garrigan and Hedrick (2003) reported that 5–10 generations were required to genetically detect bottlenecks. Moreover, Dinerstein and McCracken (1990) did not see bottleneck effects in the greater one-horned rhinoceros by using microsatellite DNA, despite well-documented evidence. Consequently, conclusions on the genetic structure of populations should not be based on molecular evidence alone but should accompany field observations. Third, polyandry, if common, and especially when combined with sperm storage, could have increased the effective population size (Sugg and Chesser 1994). Sperm storage for up to 3 years has been documented in the desert tortoise (Palmer et al. 1998) and anecdotal evidence suggests that it may occur for much longer. (One isolated captive female tortoise produced viable clutches for 15 years after her last known association with a male tortoise; P. Gould Glasco, *pers. comm.*, May 2006.) A controlled investigation of polyandry in the western Mojave Desert found that all females produced polyandrous clutches over a period of 2 years (Murphy, Edwards, Bratton, and Hagen, in prep.). And fourth, the observed increase in heterozygosity in the Northeastern Mojave and Upper Virgin River recovery units may also be a reflection of translocated tortoises. The translocation of gravid females or those that were storing sperm would serve to compound the possible explanations for excess heterozygosity.

Human-Mediated Translocations. — Translocations and releases of animals, especially if uninformed, can have negative genetic consequences (Allendorf and Luikart 2007). The historical releases and translocations of tortoises could have affected our results in the form of deviations from the H-W, increased heterozygosity and estimates of recent gene flow, anomalous distributions of some haplotypes, and increased Φ_{IS} values (through a Wahlund effect). The geographically disjunct occurrence of some haplotypes (MOJ-A01 with -B01 and -B03 in the Upper Virgin River; Table 3) could be caused by translocations. Because the widespread MOJ-A01 haplotype was absent in our initial survey of 7 tortoises in the Northeastern Recovery Unit only, we sequenced 40 additional samples: in total, 40 were MOJ-B01, 6 were MOJ-B03, and 1 was MOJ-B02. Because MOJ-A01 was absent from the Northeastern Recovery Unit, its presence in Upper Virgin River Recovery Unit was likely because of relocated tortoises. Our samples from the Northeastern Mojave were taken from relatively remote areas where the releases of captives were less likely.

Several other incidences of geographic mixing are evident: MOJ-B01 is geographically and genealogically associated with other members of Haplogroup B, but it also occurs in sympatry with Haplotypes MOJ-A01 (Haplogroup A) in the Western Mojave Recovery Unit (Table 3), specifically at the Interpretive Center at the Desert Tortoise Research Natural Area. This finding is concordant with documentation of multiple captive tortoise releases at the Natural Area (Howland 1989; Ginn

1990; Jennings 1991; Connor and Kaur 2004). Haplotype MOJ-B01 also occurs with MOJ-A01 in the Eastern Colorado Recovery Unit. Very long distance dispersion is the alternative explanation for the widespread occurrence of some haplotypes. Given the extent of documented translocations, the dispersion hypothesis is unlikely, particularly because our data lack other evidence of population expansion or recent ancestry.

Translocated tortoises could compromise the genetic integrity of a population by disruption to coadapted gene complexes in local environments or loss of fitness through outbreeding depression. In particular, Beaver Dam Slope, Utah, has a high frequency of released captive tortoises (Woodbury and Hardy 1948, Minden 1980, Minden and Keller 1981). Although we do not have genetic samples from this area, the excess of heterozygotes in the adjacent Upper Virgin River and Northeastern Mojave recovery units, in the absence of a decrease in the ratio of the total number of alleles to the overall range in allele size, could reflect first- or second-generation offspring from translocated tortoises. A similar problem may exist at the Desert Tortoise Research Natural Area and Joshua Tree National Park in the Western Mojave Recovery Unit. Outbreeding depression can lead to reduced fitness via disease in hybrid populations (Goldberg et al. 2005, Allendorf and Luikart 2007). The high levels of assignments of tortoises to the correct region (Table 7) indicate that, in some cases, survival rates of released tortoises may be low, e.g., the early California reintroduction experiments (Cook et al. 1978; Cook 1983; Weber et al. 1979).

Regional Differentiation. — The STRUCTURE analysis identified from 5 to 8 genetically structured units. These findings support the hypothesis of population structure in the *Recovery Plan* and the Desert Wildlife Management Units described in the Western Mojave Recovery Unit. When considering the close geographic proximity of some of our sample groups (e.g., groups 12 and 13), this result was consistent with our assumption that the Mojave population is genetically structured and that these genetic data were informative for designating recovery units. Sample group 8 may have the most admixture between the "Central" and "Southern" areas of the Western Mojave Recovery Unit. This subanalysis suggested that the Western Mojave Recovery Unit could be subdivided into at least 3 geographic groups. Although STRUCTURE is not a good measure of structure in populations that exhibit nonlinear patterns of IBD (Pritchard et al. 2000), the findings were congruent with the *Recovery Plan* and natural barriers to gene flow. Thus, we used these results as evidence for the assessment of recovery units.

The null hypothesis of a single, homogeneous, panmictic Mojave population was rejected. Although most alleles were broadly distributed, most sample groups significantly differed from one another in allelic frequencies (Table 7). Because the G-based exact test is sensitive to different sample sizes, as in our data, the imbalance in samples might have accounted for the high number of significant differences. However, this does not appear to be true. Most individuals ($> 80\%$) were reassigned (Table 7) back to their sample group. The accuracy of the assignments implies genetic divergence.

The population assignment was viewed as a conservative result. Our data set was limited to 11 variable microsatellite loci only. Additional loci would have likely increased the accuracy of the assignments and the distinctiveness of each recovery unit.

Congruent patterns of genetic differentiation from different regions or taxa lend credence to conclusions. Comparatively, desert tortoises from Mojave and Sonoran populations had almost identical genetic structuring at local and regional levels. The AMOVA of microsatellites from the Sonoran population revealed that 96.3% ($p < 0.001$) of the diversity occurred in individuals within study sites ($\Phi_{IT} = 0.963$), whereas only 3.7% ($p < 0.001$) of the variation was among sites ($\Phi_{ST} = 0.037$) (Edwards et al. 2004). The same result occurred in a geographically equivalent sized subset of our data; $\Phi_{ST} = 0.037$ ($p < 0.001$). In both studies, a significant positive correlation occurred between genetic distance (pairwise Φ_{ST}) and geographic distance.

Recovery Units Revisited

The authors of the *Recovery Plan* proposed 6 recovery units to capture the known genetic, morphological, ecological, and behavioral diversity in desert tortoises as of 1993 (USFWS 1994). Their original objectives agree with the views of Crandall et al. (2000), specifically to preserve the options for adaptive diversity and evolutionary processes, maintain a network of populations, reduce the likelihood of further contraction of the geographic range, and minimize homogenization of the gene pool or pools by anthropogenic activities. The recovery units in the *Recovery Plan*, with some exceptions described below, appear to reflect natural, biological differences in populations and to fall within the DPSs described in government policy (US Department of the Interior and US Department of Commerce 1996).

We emphasize, however, that the genetic evidence presented here is not necessarily concordant with or related to morphological, ecological, and behavioral differences observed in the tortoise populations. Genetic evidence is only one factor among many that should be considered in managing desert tortoises (Crandall et al. 2000; DeSalle and Amato 2004; Green 2005). No direct evidence suggests that the mtDNA and microsatellite markers reflect the observed phenotypic differences and local adaptations, although the assumption is that identified genetic markers may serve as surrogates for these and other character traits (Pearman 2001). Behavioral differences between populations can be genetically linked, as in the case of garter snake food habits (Arnold 1981) and morphological variability in turtles can be heritable (Myers et al. 2006).

In the absence of data linking genotypic markers with specific phenotypic characters or adaptations in desert tortoises, we are confined to delineating recovery units based on available information, such as the differences in mtDNA and microsatellite markers described here, as well as differences in vegetative communities, physical attributes of the habitat, climate (e.g., mean number of freezing days annually, mean annual precipitation, amounts of precipitation occurring in summer), choice and availability of forage plants, cover sites (burrows, dens), and denning behavior.

The direct translation of molecular data into management units is subjective. On one extreme, it is possible to define 2 recovery units, based on the arbitrary subdivision of assignment values. However, the STRUCTURE analysis indicated the presence of at least 6 genetically cohesive units. Although this evaluation was compromised by multidimensional IBD, when we reduced the effects of IBD, 4 additional genetic units were identified in the Western Mojave Recovery Unit: sample groups 1–2, 3–5, 8, and 6–7 plus 9–10 (Fig. 4). Ultimately, the designation of recovery units must synthesize all relevant factors to achieve effective management.

Our analyses indicate that the Western Mojave Recovery Unit should be divided into 3 regions (western, southern, and central) and 3 corresponding recovery units: Western Mojave, Central Mojave, and Southern Mojave (Table 8, Fig. 7). Although the analysis by using STRUCTURE discovered 4 genetic units within the Western Mojave, the segregation of 1 site (8) would not facilitate effective management. Our proposed recovery units are similar to the 3 Desert Wildlife Management Areas described in the *Recovery Plan* and are concordant with the western, southern, and central regions of the Mojave Desert described by botanists and climatologists (Rowlands et al. 1982; Rowlands 1995a, 1995b). The western, central, and southern Mojave regions differ primarily in the amounts of summer rainfall, number of freezing days, and mean January minima and mean July maxima temperatures, as well as in species richness (vegetation) and types and composition of plant species with different metabolic pathways, e.g., C_3, C_4, and Crassulacean acid metabolism (CAM). The redefined Western Mojave Recovery Unit (Fig. 7) receives precipitation primarily in winter and $< 10\%$ of rainfall occurs in summer (Rowlands 1995a; Table 8). The summer flora is very limited, and tortoises rely heavily on the succulent green forbs and herbaceous perennial plants available in late winter and spring (Jennings 1993, 2002; Oftedal 2002; Oftedal et al. 2002). The proposed Central Mojave Recovery Unit is the hottest and driest of the 3 regions and is low in botanical diversity (Rowlands, 1995a). Of the 3 regions, the proposed Southern Mojave Recovery Unit has more summer precipitation and a higher richness of C_4 and CAM plant species (Rowlands 1995a). Until ca. 100 years ago, the Southern Mojave Recovery Unit was physically separated from the proposed Central Mojave and Western Mojave recovery units by the Mojave River; human activities have since reduced or eliminated the flow along much of the river.

Climatic differences between all recovery units profoundly affect timing and availability of forage, as well as seasonal activities and very possibly depth of burrows and, thus, protection from freezing temperatures and the hot, dry summers. The existing eastern recovery units in the Mojave population have higher percentages of precipitation in the summer, thus supporting a more diverse and complex summer flora (Table 8; Rowlands 1995a, 1995b; Oftedal 2002). A winter flora is also available. Differences in the mean number of freezing days per annum contribute to seasonal activity periods and the types of winter hibernacula protecting the tortoises from freezing. The Northern and Eastern Colorado Desert recovery units are the warmest, with 1–16 freezing days/y compared with 29–127 freezing days/y in the Mojave. Northeastern recovery units are by far the coldest, possibly contributing to the well-developed dens and lengthy tunnels on Beaver Dam Slope (Woodbury and Hardy1948) that are rarely observed outside the Northeastern Mojave and Upper Virgin River recovery units.

Genetic assignments do not support a separation between the Eastern Mojave and Northern Colorado recovery units, possibly because we only had 4 sample groups from these regions. The close geographic proximities of the sample groups (Fig. 7) are unlikely to reflect the potential diversity occurring along a 250 km north-south axis. Until more data are gathered along the north-south axis, we do not recommend treating the 2 recovery units as one, because of major differences in climate, forage availability, and seasonal activities. These distinctions may be exactly the kind of ecological/adaptive differences worthy of conservation management, independent of the units delimited by neutral molecular variation (Crandall et al. 2000; Allendorf and Luikart 2007). Significantly, unlike the genetically restricted and legally inapplicable ESU, the legal application of DPS allows for and promotes such protection (US Department of the Interior and US Department of Commerce 1996).

The Northeastern Recovery Unit (group 11) and the Upper Virgin River Recovery Unit (group 15) showed the strongest differentiation (MDS plot, assignment test, and unique matriarchal lineage). They may be more genetically isolated than other areas. Both potentially show evidence of recent population reductions. Additional sampling of these regions is encouraged for evaluation of current management strategies. Unfortunately, under current legislation these and perhaps other demes cannot be protected solely on the basis of the degree of threat alone, as recently advocated by Green (2005).

Recovery Actions. — Populations that have become disjunct or mixed as a result of recent anthropogenic activities may be suitable for restorative actions (Crandall et al. 2000; Allendorf and Luikart 2007). One restorative action would be to remove deliberately or inadvertently

Table 8. Physical and biological attributes of proposed recovery units for the Mojave population.

Recovery unit	Mean annual precipitation (mm)	% Rainfall June–Sept	Mean no. freezing days annually	Mean July maximum temperature (°C)	Topography	Vegetation types
Western Mojave	90–150	3.1–9.9	33–84	35.4–37.4	Flats, valleys, alluvial fans, rolling hills, mountainous slopes	(1) Creosote Bush Scrub, (2) Mojave Saltbush-Allscale Scrub (endemic), (3) Indian Rice Grass Scrub-Steppe, (4) Hopsage scrub, (5) Cheesebush scrub (west Mojave type)
Central Mojave	109	18.3–20.7	57 +	39.1–42.9	Flats, valleys, alluvial fans, rolling hills, mountainous slopes, rock outcrops, badlands, sand dunes, lava flows	(1) Creosote Bush Scrub, (2) Big Galleta Scrub Steppe, (3) Hopsage Scrub, (4) Cheesebush scrub, (4) Desert Psammophytes
Southern Mojave	108	18.1–36.1	29–104	37.2–39.1	Flats, valleys, alluvial fans, rolling hills, mountainous slopes, rock outcrops, lava flows	(1) Creosote Bush Scrub, (2) Big Galleta Scrub Steppe, (3) Hopsage Scrub, (4) Cheesebush scrub, (4) Desert Psammophytes, (5) Blackbush Scrub
Eastern Mojave	112–208	27.5–37.7	34 +	34.8–36.1	Flats, valleys, alluvial fans, bajadas, rocky slopes	(1) Big Galleta-Scrub Steppe, (2) Succulent Scrub (*Yucca*, *Opuntia*), (3) Creosote Bush Scrub, (4) Cheesebush Scrub (eastern Mojave type), (5) Indian Rice Grass Scrub-Steppe
Northeastern Mojave	100–210	27.1–41.0	46–127	38.2–40.1	Flats, valleys, alluvial fans, rocky slopes, deeply cut washes	(1) Creosote Bush Scrub, (2) Big Galleta Scrub-Steppe, (3) Desert Needlegrass Scrub-Steppe, (4) Blackbush Scrub
Upper Virgin River	210	28.7	96 +	38.4	Rocks, caves, sandstone crevices, sand dunes	Transitional Vegetation: (1) Sagebrush Scrub, (2) Psammophytes, Great Basin (sand sage), (3) Blackbush Scrub
Northern Colorado	112–129	32.6–34.1	2–12	42.2–42.3	Flats, valleys, bajadas, rocky slopes, small washes	(1) Succulent Scrub (*Fouquieria, Opuntia*, *Yucca*), (2) Blue Palo Verde-Smoke Tree Woodland, (3) Creosote Bush Scrub (lava flows)
Eastern Colorado	96–100	32.3–34.4	1–16	40.5–42.2	Flats, valleys, alluvial fans, small washes, deeply dissected washes, rocky slopes	(1) Succulent Scrub (*Fouqueria, Opuntia, Yucca*), (2) Blue Palo Verde-Ironwood-Smoke Tree Woodland, (3) Creosote Bush Scrub (rocky slopes)

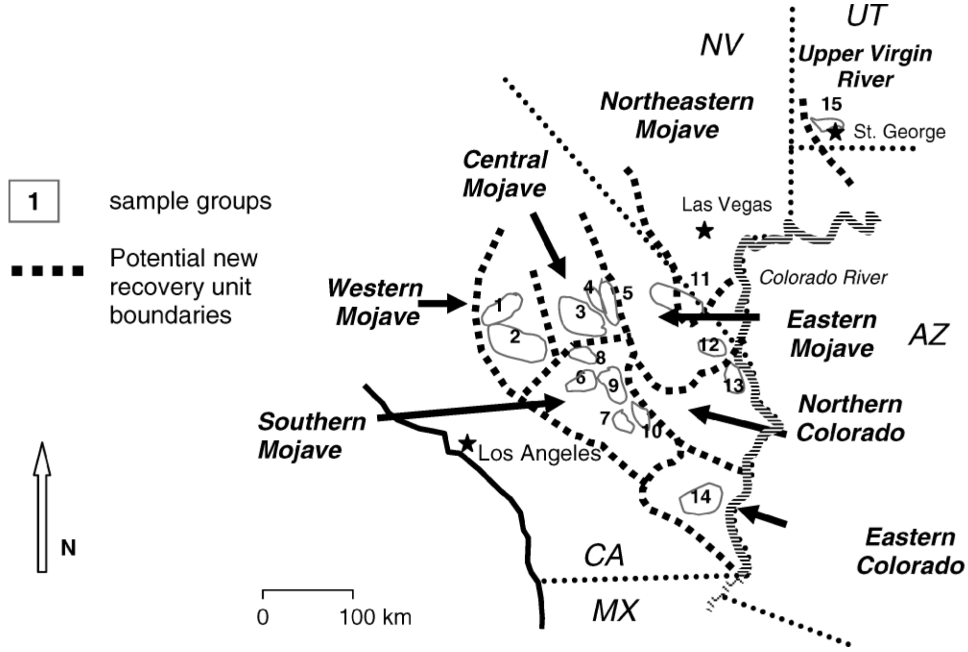

Figure 7. Sample groups of desert tortoises, *Gopherus agassizii*, shown with a new, preliminary alignment of recovery unit boundaries developed by using the mitochondrial deoxyribonucleic acid and microsatellite data presented in this study.

translocated tortoises from critical habitat. This strategy would be unreasonably difficult where populations are dense but may be a viable option where the area of interest and densities are limited, populations are declining, and most tortoises could be located and sampled. This strategy might be appropriate in the Upper Virgin River Recovery Unit and the Beaver Dam Slope Desert Wildlife Management Area (within the Northeastern Mojave Recovery Unit). Another restorative action would be to genetically test tortoises in the vicinity of frequently used recreation sites within national parks, research natural areas, and other protected areas: sites where visitors often release tortoises illegally, e.g., the Desert Tortoise Research Natural Area. The released tortoises from other populations could be identified and removed to a more appropriate place. In populations that have dropped below viable levels (e.g., Fremont-Kramer Desert Wildlife Management Area, Western Mojave Recovery Unit), informed and carefully planned augmentations or translocations could promote recovery, as has been done for a few other species (Allendorf and Luikart 2007). However, genetic planning is an essential part of such recovery efforts. Using tortoises within a well-defined recovery unit or local geographic area for headstarting or augmentation is far more desirable than translocating tortoises between recovery units. If local adaptations exist, then uninformed translocations of desert tortoises may do much more harm than good by introducing maladaptive genes into a locally adapted population.

Empirical studies need to be designed and tested to determine whether marker loci reflect specific adaptations with potential conservation value. For the Mojave population of the desert tortoise, the initial recovery units were defined on the basis of morphological, ecological, and behavioral differentiation, and the patterns of genetic variation parallel the earlier assessment in the *Recovery Plan*. Taken together, these 2 independent approaches strongly suggest the occurrence of local adaptation and evolutionary potential. Not only is it essential that this potential be conserved but also that underlying hypotheses be tested in the near future.

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CURRENT STATUS OF THE MOHAVE GROUND SQUIRREL

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ABSTRACT: The Mohave ground squirrel (*Spermophilus mohavensis*) is found only in the western Mojave Desert of California. Although it is listed as Threatened by the State of California, there is little published information regarding its current distribution and status. I have assembled a comprehensive database covering unpublished field studies, surveys, and incidental observations conducted over the 10-year period from 1998-2007. This database contains records of 1140 trapping sessions, only 102 of which were successful in capturing ≥1 Mohave ground squirrels. In addition, there are 96 incidental observations in which the species was detected. An analysis of these 198 positive records identifies 4 core areas that continue to support relatively abundant Mohave ground squirrel populations and 4 other areas in which there are multiple recent records of the species. Although the southern portion of the range has been most intensively sampled, the only recent occurrences there are from a single core population on Edwards Air Force Base plus an additional 4 detections from Victor Valley. There are extensive areas within the geographic range where the status of the species is unknown, especially on the China Lake Naval Air Weapons Station and Fort Irwin. I present recommendations for surveys in areas where no recent studies have been carried out. I also identify potential corridors between known populations and recommend studies to determine if these connections are actually occupied by the species. Finally, I indicate conservation measures needed to ensure that known populations and corridors are adequately protected from habitat loss and degradation.

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Key words: Mohave ground squirrel, *Spermophilus mohavensis*, California, Mojave Desert, threatened species, core populations, corridors, conservation

The Mohave ground squirrel (*Spermophilus mohavensis*) is found only in the western Mojave Desert of California (Best 1995). Its historic range (Figure 1) totaled about 20,000 km^2 (Gustafson 1993). It has been found from the area of Palmdale and Victorville in the south to Owens Lake in the north. The eastern escarpment of the Sierra Nevada forms much of the western boundary of its range, while in the east its distribution extends to the Mojave River Valley and to the Fort Irwin military reservation. This region has experienced rapid growth over the past few decades. Urban development in the Antelope Valley, Indian Wells Valley, and along the Mojave River from Victorville to Barstow has resulted in a human population in excess of 700,000. Three large military bases conduct extensive training and testing operations. Much of the western Mojave Desert is used for motorized outdoor recreation, mining, and livestock grazing. There is an expanding transportation infrastructure, including highways, railroads, airports, pipelines, and electric transmission lines. Recent government policies have stimulated great interest in siting renewable energy facilities in this region, especially wind farms and solar installations.

Because of these multiple development pressures, there has been significant and on-going loss of wildlife habitat in the western Mojave Desert as well as widespread habitat degradation and fragmentation. There has been concern about the conservation status of the Mohave ground squirrel since 1971, when it was first listed as Rare under the California Endangered Species Act (CESA). After the reauthorization of CESA in 1984, the species was classified as Threatened. Its subsequent regulatory history has been highly controversial. In 1993, the California Fish and Game Commission acted to remove it from the list of threatened species, a decision that was set aside in 1997 following judicial review. A petition to list the Mohave ground squirrel under the federal Endangered Species Act (ESA) was rejected by the US Fish and Wildlife Service in 1995. The US Fish and Wildlife Service is currently (2008) reviewing a new petition to list the species as endangered under the ESA.

In 2006, the US Bureau of Land Management (BLM) approved the West Mojave Plan, which was designed to conserve a number of sensitive species throughout the western Mojave Desert, with special emphasis on the desert tortoise (*Gopherus agassizii*) and Mohave ground squirrel (Bureau of Land Management 2006). The alternative version of the plan as adopted established a Mohave Ground Squirrel Conservation Area consisting of 6,988 km^2 of public lands managed by the BLM. (Fig. 1) These conservation measures do not apply to private and military lands within the historic range of the species.

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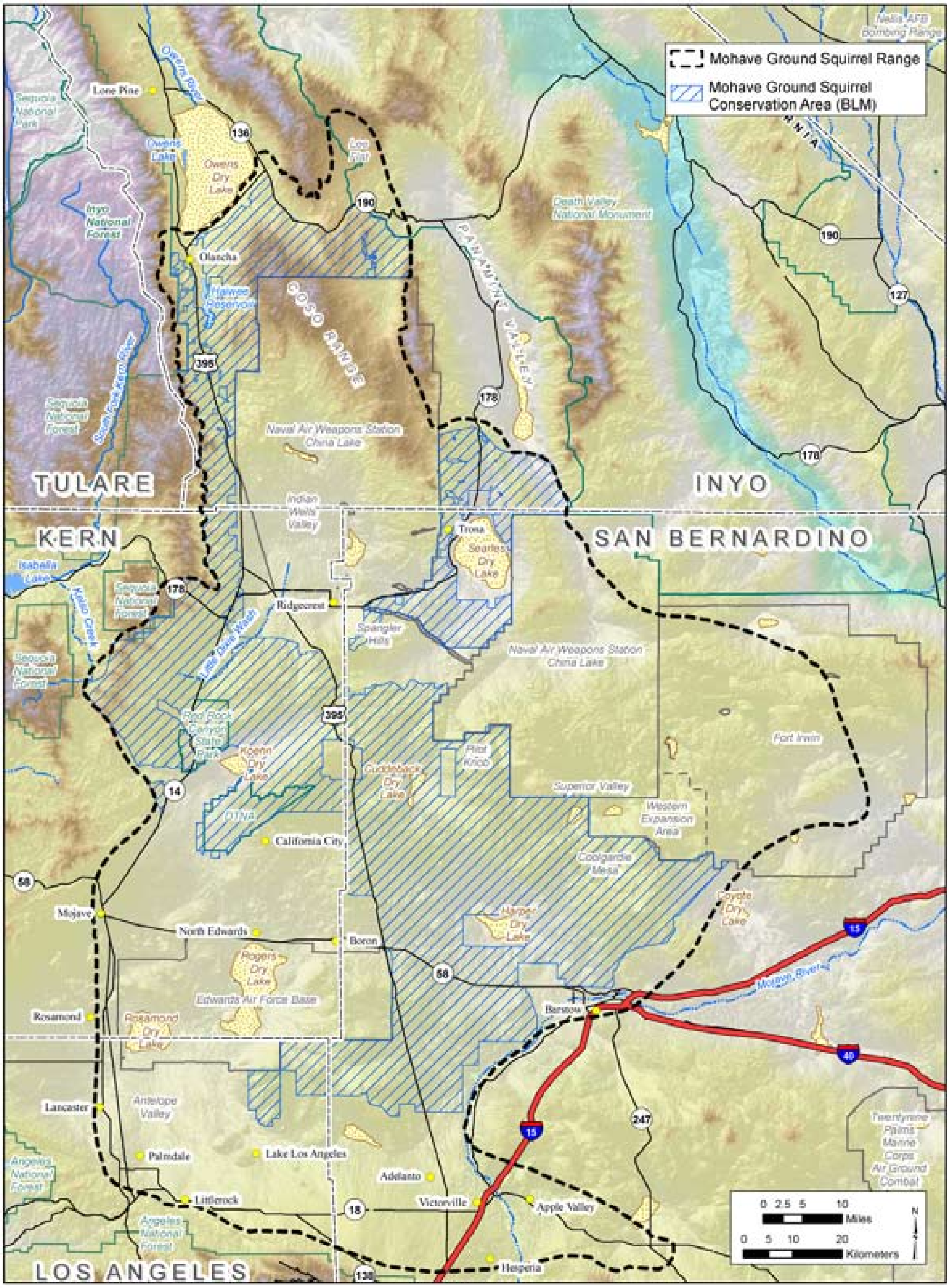

Figure 1. The historic range of the Mohave ground squirrel in the western Mojave Desert of California, with important place names indicated. The Mohave Ground Squirrel Conservation Area is shown as established in the West Mojave Plan (U.S. Bureau of Land Management (2005).

Although the Mohave ground squirrel has been designated as a state-listed species since 1971 and has been the focus of a major conservation planning effort by the BLM, there is still little published information on its distribution, abundance, and population trends. Brooks and Matchett (2002) reviewed 19 reported studies of the species, covering the period from 1918 to 2001. Only 2 of these studies were published in scientific journals. Since this review by Brooks and Matchett, a great deal of new information has become available, most of it unpublished. Two radiotelemetry studies describing home range dynamics and juvenile dispersal were recently published in peer-reviewed journals (Harris and Leitner 2004, 2005). Several state and federal agencies, as well as private conservation groups, have sponsored field research designed to determine the status of the species in particular areas. In addition, the California Department of Fish and Game (CDFG) requires trapping surveys at proposed development sites according to a prescribed protocol (CDGF 2003).

This paper brings together the data from unpublished field studies and surveys conducted during the 10-year period from 1998-2007. I have obtained reports for all sponsored research surveys and have received information on protocol trapping surveys from many consulting biologists. The information presented here includes both positive records documenting Mohave ground squirrel occurrence and negative results from trapping surveys in which the species was not detected. The objectives of this review are to:

1. Document the geographic distribution of Mohave ground squirrel occurrences,
2. Summarize the distribution and relative intensity of survey efforts,
3. Identify important areas and corridors for conservation based on available occurrence data, and
4. Recommend areas where additional survey effort is needed.

METHODS

I utilized 4 sources of information regarding the distribution and occurrence of the Mohave ground squirrel during the period 1998-2007: the California Natural Diversity Database, regional field studies, protocol trapping at proposed development sites, and incidental observations as reported by field biologists.

The California Natural Diversity Database (CNDDB) is a state-wide inventory of the status and locations of rare species and natural communities. The CDFG produces and regularly updates this computerized catalog, which contains records of occurrence submitted by state and federal agencies, consulting firms, and individual biologists. It contains positive records of occurrence only and generally does not include data documenting the absence of a species from a particular locality.

The CNDDB contained a total of 293 occurrence records for the Mohave ground squirrel as of August 4, 2007 (CNDDB 2007). Twenty-eight new occurrences were submitted during the period from 1998-2007 and there were also 2 new records at previously known locations for the species. These records were obtained from regional field studies, protocol trapping, and incidental observations. I incorporated these 30 records into the data base used in this analysis.

A number of regional field studies have been conducted during the past 10 years, many of them funded by public agencies and private conservation groups. I have reviewed 19 unpublished reports that describe the results of such trapping surveys and have also obtained data from several biologists whose surveys have not been documented in formal reports (Appendix A).

The third source of data was trapping surveys carried out at proposed development sites, as required by the CDFG (CDFG 2003). The CDFG guidelines specify that surveys be conducted on proposed project sites that support desert scrub vegetation and are within or adjacent to the Mohave ground squirrel geographic range. The surveys must be carried out by a qualified biologist operating under authority of a Memorandum of Understanding (MOU) with CDFG. The protocol mandates an initial visual survey of the project site. If no Mohave ground squirrel is detected visually, live-trapping is required for up to 3 sessions of 5 consecutive days each. The trapping sessions must be conducted during the periods March 15-April 30, May 1-31, and June 15-July 15. Trapping grids normally consist of 100 traps arranged in a 4x25 array (linear projects) or in a 10x10 array (other projects).

If a Mohave ground squirrel is detected on the site, the project proponent must apply to CDFG for an Incidental Take Permit and provide compensation, usually in the form of mitigation lands. If no Mohave ground squirrel is observed or captured, it is not necessarily evidence that the site is unoccupied or is not potential habitat. Nonetheless, CDFG will stipulate for a period of 1 year that the project site harbors no Mohave ground squirrels. Most protocol surveys carried out in recent years have not resulted in detection of the species.

In order to obtain the results of protocol trapping surveys for the period 1998-2007, I contacted all biologists who were known to possess an MOU authorizing take of Mohave ground squirrels. The great majority responded by providing their survey data, including dates of trapping sessions, coordinates of grid centers, number of trap-days of sampling effort, and whether or not Mohave ground squirrels were detected. Although I have not obtained data for all protocol trapping efforts, I have collected a total of 943 records that represent 426,615 trap-days of sampling. I estimate that I obtained records for >95% of the total protocol trapping effort for the period 1998-2007.

I have classified as incidental observations all reports by biologists who observed or captured Mohave ground squirrels incidental to other field studies. This category includes visual and auditory detections, captures made while trapping for other species, and highway mortalities.

For regional and protocol surveys, a record is defined as a single trapping session, usually consisting of 5 successive days. Records from trapping surveys can be negative, with no Mohave ground squirrel captures, or positive, indicating a session with at least 1 capture. On the other hand, records from incidental observations were always positive, indicating the detection of at least 1 Mohave ground squirrel at a specific location. Table 1 lists the number of records obtained for this review from regional surveys, protocol trapping, and incidental observations. The regional and protocol trapping surveys provided a total of 1,038 negative records, as compared to only 102 trapping sessions in which at least 1 Mohave ground squirrel was captured. Although the regional studies involved only 21.6% of the total trapping effort, they accounted for 69.6% of the positive records. On the other hand, the protocol surveys made up 78.4% of trapping effort, but contributed only 30.4% of Mohave ground squirrel detections.

Table 1. A summary of the data sources used for this review. For regional and protocol surveys, a record is defined as a single trapping session (usually 5 days) at a specific grid location. If no Mohave ground squirrels were detected, such records were considered negative, while a positive record was a trapping session in which >1 Mohave ground squirrels were captured. For incidental observations, all records are positive. Each record indicates the detection of >1 Mohave ground squirrels at a particular location. The sampling effort for regional and protocol surveys is calculated as the number of traps operated per day times the number of days per trapping session summed over all trapping sessions.

Type of Data	Total	Positive Records	Trap-days
Regional Surveys	197	71	111,710
Protocol Surveys	943	31	426,615
Incidental Observations	96	96	N/A
Totals	1,236	198	538,325

I entered data from all sources into an Excel spreadsheet and then imported that into an Access database. This permitted data to be manipulated and extracted through the query process. A series of base maps covering the geographic range of the Mohave ground squirrel was developed using Geographic Information System (GIS) techniques. All records, both positive and negative, were plotted on these digital maps for visual analysis. In this way, the distribution of Mohave ground squirrel occurrences for the last 10 years could be visualized in relation to the distribution of sampling effort.

RESULTS

General Distribution of Mohave Ground Squirrel Records

The geographic distribution of both positive and negative Mohave ground squirrel records over the period 1998-2007 is shown in Figure 2. There has been no attempt at either systematic or random range-wide sampling and the records tend to be concentrated in certain well-defined regions. The great majority of trapping effort has been conducted in the southern part of the geographic range, south of State Route 58. In spite of this very intensive sampling, Mohave ground squirrels have been detected in only 2 areas south of State Route 58, one on Edwards Air Force Base and the other in the vicinity of Victorville. The northern part of the geographic range is in Inyo County, where almost all trapping has been conducted in the Coso region on China Lake Naval Air Weapons Stations (China Lake NAWS) and in the vicinity of Olancha and Haiwee Reservoir. Outside of these 2 areas, there have been only 5 widely scattered detections in the entire northern part of the range over the past 10 years. In the central part of the range, from Ridgecrest south to State Route 58, most positive records have been concentrated in 6 distinct regions. Trapping in the vicinity of Ridgecrest has resulted in the capture of a number of Mohave ground squirrels and there are abundant records for the extensive valley (Little Dixie Wash) between Inyokern and Red Rock Canyon State Park. To the south, there is a cluster of detections associated with the Desert Tortoise Natural Area (DTNA) and another in the Pilot Knob region east of Cuddeback Dry Lake. There are many records from the broad plateau that lies north of Barstow (Coolgardie Mesa and Superior Valley) and there are also several detections in the area just north of Boron.

It is clear that there are extensive areas within the range of the Mohave ground squirrel that have not been

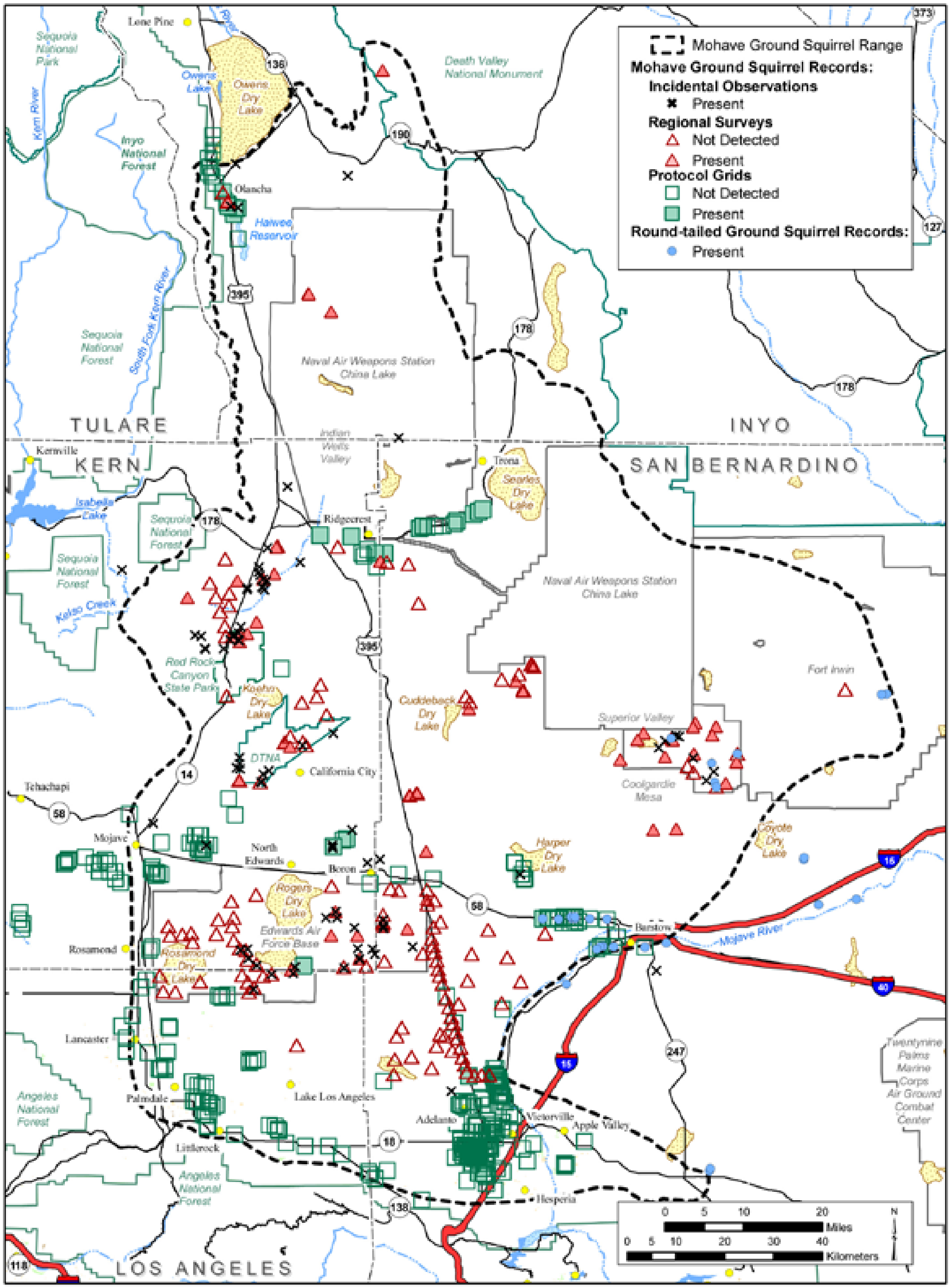

Figure 2. The geographic distribution of all Mohave ground squirrel records for the period 1998-2007. A total of 1,236 records are plotted, which include 1,140 trapping sessions conducted for regional and protocol surveys and 96 incidental observations. Solid triangles and squares represent locations of trapping grids at which >1 Mohave ground squirrels were captured. Crosses show sites of the 96 incidental observations at which >1 Mohave ground squirrels were detected.

effectively sampled. Figure 3 shows a 10x10 km sampling frame superimposed on the geographic range, with the sampling units color-coded to indicate the number of records (both positive and negative) for each unit during the period 1998-2007. It can be seen that sampling efforts have been heavily concentrated in the southern part of the range, especially to the west and north of Victorville, in the Palmdale-Lancaster area, around Barstow, and in the vicinity of the town of Mojave. Approximately 67% of all trapping efforts have been located in the region from State Route 58 south. The lack of recent data on Mohave ground squirrel occurrence in the northern part of the range is obvious, but there are also large gaps in our knowledge in the central part of the range. Except for the Coso area, there have been no surveys on either the north or south ranges of China Lake NAWS during the past 10 years. The Western Expansion Area of Fort Irwin has been well sampled using a randomized method of selecting trapping sites. However, only 1 trapping attempt has been recorded elsewhere on Fort Irwin over the period 1998-2007. In contrast, Edwards Air Force Base has sponsored extensive surveys on a randomized sampling basis, so that the distribution of the species is known there in great detail.

Regional Analysis of Mohave Ground Squirrel Records

In this section, I present detailed information on Mohave ground squirrel distribution and abundance during the period 1998-2007 for a number of regions within the geographic range. This regional analysis is supported by a series of 7 maps that are available as Supplemental Online Material at the website of The Western Section of The Wildlife Society: http://tws-west.org/transactions/TWSWS_Transactions_directory.htm

Inyo County.—Inyo County includes the northernmost region occupied by Mohave ground squirrels. Records are concentrated in the area between Olancha and Haiwee Reservoir and in the Coso Range, within the China Lake NAWS. The species has been detected at 5 protocol trapping grids to the south of Olancha, beginning in 2002. Mohave ground squirrel populations at 2 sites in the Coso Range have been monitored by regular spring trapping sessions. Animals have been captured on both grids at every trapping occasion. In 2007, a Mohave ground squirrel was captured at Lee Flat just inside the boundary of Death Valley National Park, which marks the northernmost record for the species. The other 4 records for Inyo County are incidental observations, including an individual that was stuck by a vehicle in northern Panamint Valley, several kilometers east of the generally-accepted limits of the range.

Ridgecrest Area.—Trapping has been conducted at 10 grids in the vicinity of Ridgecrest, with Mohave ground squirrels detected at 5 of these sites. In addition, protocol trapping at 10 grids along State Route 178 east of Ridgecrest in 2006 yielded captures at 6 locations. However, no Mohave ground squirrels were captured in 2002 at 2 sites in the Spangler Hills southeast of Ridgecrest.

Little Dixie Wash.—The Little Dixie Wash region is a broad valley extending from Inyokern southwest to Red Rock Canyon State Park. Two extensive trapping studies have detected Mohave ground squirrels throughout this region. In 2002, the species was captured at 6 of 7 grids widely scattered across this valley. There have been more than 20 incidental observations as well, suggesting that Mohave ground squirrels are widely distributed here. In 2007, a visual sighting established the first record to the west of the mountain crest in the Kelso Creek drainage.

Fremont Valley to Edwards Air Force Base.—The Fremont Valley extends northeast from the vicinity of Cantil toward Garlock and Johannesburg. No Mohave ground squirrels have been detected here during the past 10 years, despite trapping efforts at 6 grids. There are 13 positive records around the periphery of the DTNA and out a few kilometers to the east. No trapping has been carried out in the interior of the DTNA, but it is likely that Mohave ground squirrels are present there as well. Two incidental records exist for the area just to the north and east of the town of Mojave, but repeated protocol trapping efforts here have been unsuccessful. Finally, there are 10 trapping records and incidental observations in the area to the north of Boron and Kramer Junction. These records suggest a fairly widespread population across this region.

Wind Farm Area Southwest of Mojave.—Protocol trapping surveys have been conducted at 24 grids located on wind energy development sites southwest of the town of Mojave. Although this area is outside the generally-accepted boundaries of the geographic range, much of the habitat here seems suitable for the species. To date, no Mohave ground squirrels have been detected during these trapping efforts. Two recent visual observations are listed in the CNDDB, but confirmation through trapping is needed.

Edwards Air Force Base.—Edwards Air Force Base has been carrying out an extensive monitoring program to document the distribution of Mohave ground squirrels within the military reservation. From 2003 through 2007, trapping has been conducted at 40 randomly-located grids across the base, resulting in detection of the species at 6 of these sites. In combination with other trapping efforts and incidental observations, this program has clearly defined the area in which Mohave ground squirrel populations are present.

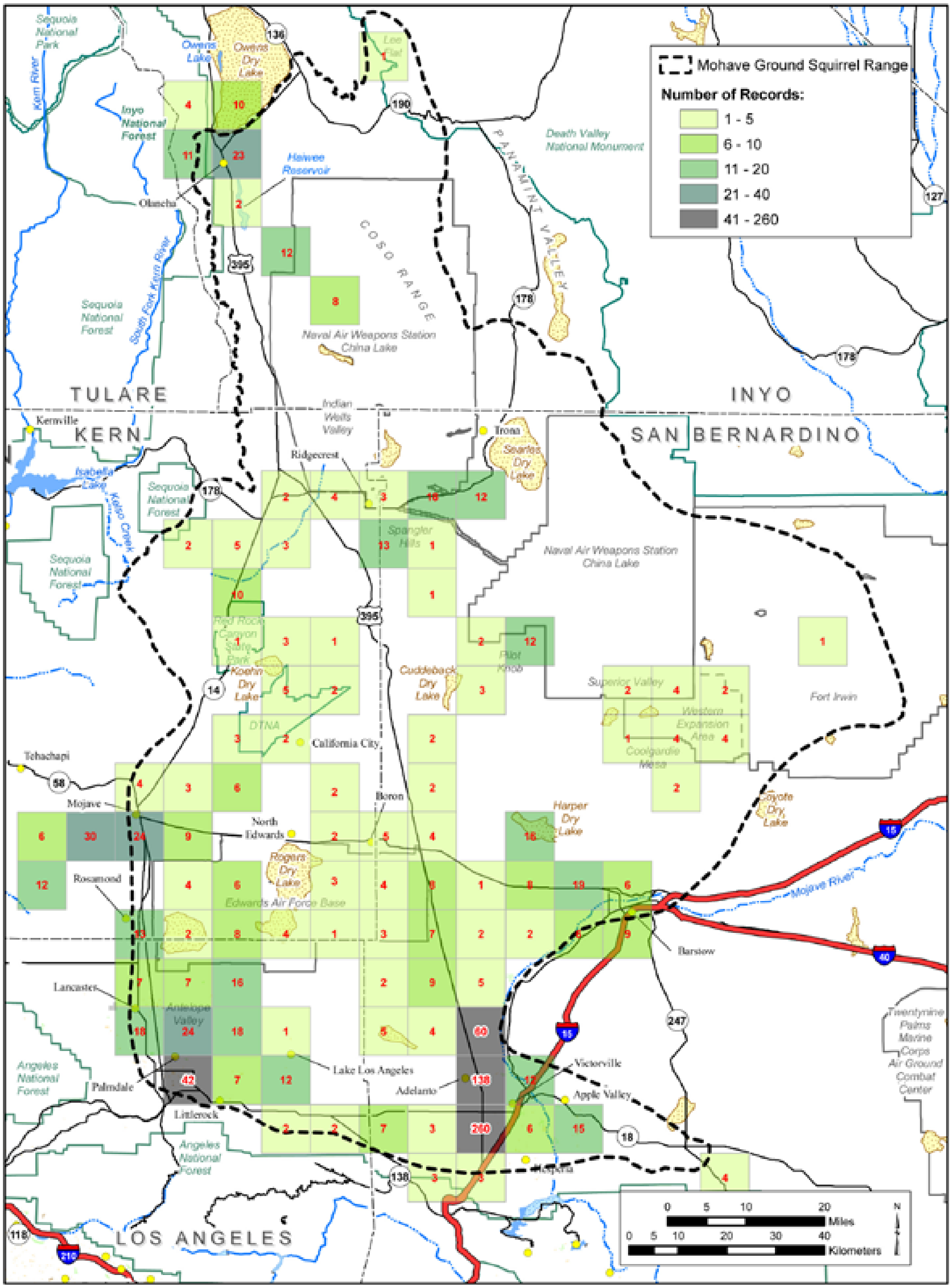

Figure 3. The distribution of sampling effort throughout the historic range of the Mohave ground squirrel for the period 1998-2007. A 10 x 10 kilometer sampling frame is set over the region and the total number of records (both positive and negative) are indicated for each 10 x 10 km block. These records are the trapping sessions conducted for regional and protocol surveys. Incidental observations are not plotted here.

Los Angeles County.—Protocol trapping has been conducted at 52 grid locations in the desert portion of Los Angeles County during the period 1998-2007, but no Mohave ground squirrels have been detected by this method. The only positive records in Los Angeles County have been 4 detections in a small area near Rogers Dry Lake on Edwards Air Force Base.

Victor Valley to Barstow.—Intensive protocol trapping has been conducted in the Adelanto area and on the western outskirts of Victorville, resulting in the capture of Mohave ground squirrels at 3 separate locations. The 2 trapping records north of Adelanto plus a visual sighting just to the west suggest the presence of a residual population in this area. Capture of a juvenile female well to the south near the intersection of US 395 and I-15 indicates that another population may exist here as well. There have been no records east of the Mojave River since 1955 but, as shown in Figure 2, this area has not been effectively sampled in the last 10 years. Three major trapping studies have been conducted from El Mirage Dry Lake north and east toward Barstow. There have been no detections of Mohave ground squirrels over this extensive area.

Barstow Area.—There were only 3 Mohave ground squirrel records in the Barstow area during the period 1998-2007. In 2005, a Mohave ground squirrel was observed about 6 km south of Barstow near the city landfill, in an area outside the generally-accepted range boundary. Two other occurrences were documented in 2007 to the west of Barstow. Mohave ground squirrels were detected at the edge of an alfalfa field near Harper Dry Lake and 1 was trapped about 10 km west of Hinkley near State Route 58.

Coolgardie Mesa and Superior Valley.—To the north of Barstow is a broad, gently-sloping plateau that extends from Coolgardie Mesa in the south to Superior Valley in the north. Three trapping studies have been conducted in this region over the past 10 years and all have documented Mohave ground squirrel occurrences. There have also been at least 7 incidental observations.

Pilot Knob Area.—Trapping studies in the Pilot Knob area, from Cuddeback Dry Lake east to the boundary of China Lake NAWS, have detected Mohave ground squirrels at 5 different sites.

Contact Zone with Round-tailed Ground Squirrel

The Mohave ground squirrel and the round-tailed ground squirrel (*Spermophilus tereticaudus*) are closely related (Hafner and Yates 1983). The 2 species are very similar in general appearance, the most obvious difference being the much longer tail of the round-tailed ground squirrel. The round-tailed ground squirrel is found throughout the eastern Mojave Desert of California and its geographic range adjoins that of the Mohave ground squirrel. The contact zone between the 2 species extends from Lucerne Valley along the Mojave River to Barstow and then northeast through Fort Irwin (Fig. 4). During the period 1998-2007, a total of 30 round-tailed ground squirrel occurrences have been recorded in this contact zone. Round-tailed ground squirrels are common in the area around Barstow, especially in disturbed habitats. The species has also been observed in Lucerne Valley, near Hodge on the Mojave River, near Coyote Dry Lake, and on the eastern side of Fort Irwin. In addition, round-tailed ground squirrels have been detected in 2 areas well within the historic range of the Mohave ground squirrel. There have been 5 reports from the Western Expansion Area of Fort Irwin, as much as 24 km inside the generally-accepted boundary of the Mohave ground squirrel range. The other area of interest is west of Barstow along State Route 58, where round-tailed ground squirrels were trapped at 8 sites in 2006 and 2007. Individuals of both species were captured on a grid about 20 km west of the range boundary. Lack of historical baseline data makes it impossible to determine if the round-tailed ground squirrel is actively extending its distribution at the expense of the Mohave ground squirrel.

DISCUSSION

General Distribution of Mohave Ground Squirrel Records

It is important to be clear about the significance of positive records that indicate Mohave ground squirrel presence during the past 10 years. These positive records are highly concentrated in just 8 distinct areas, in which 93.4% (185/198) of all Mohave ground squirrel occurrences have been documented (Fig. 5). It is of interest that there are at least some Mohave ground squirrel records prior to 1998 in each of these 8 areas, suggesting that recent trapping effort has focused on areas with historic records. However, much of the Mohave ground squirrel range has never been surveyed. This is especially true in Inyo County, which includes large areas where no surveys or protocol trapping have ever been carried out. The situation is similar, although not as extreme, in the central part of the range. There are 6 areas here where recent evidence indicates the presence of Mohave ground squirrel populations. However, little trapping has been conducted outside the areas that support these known populations. In the southern part of the range, south of State Route 58, there has been much greater trapping effort and the sampling has been much more widely distributed. Even here, there are still a few relatively restricted areas that have not been surveyed since 1998. In all 3 sections of the Mohave ground squirrel range, additional populations may well

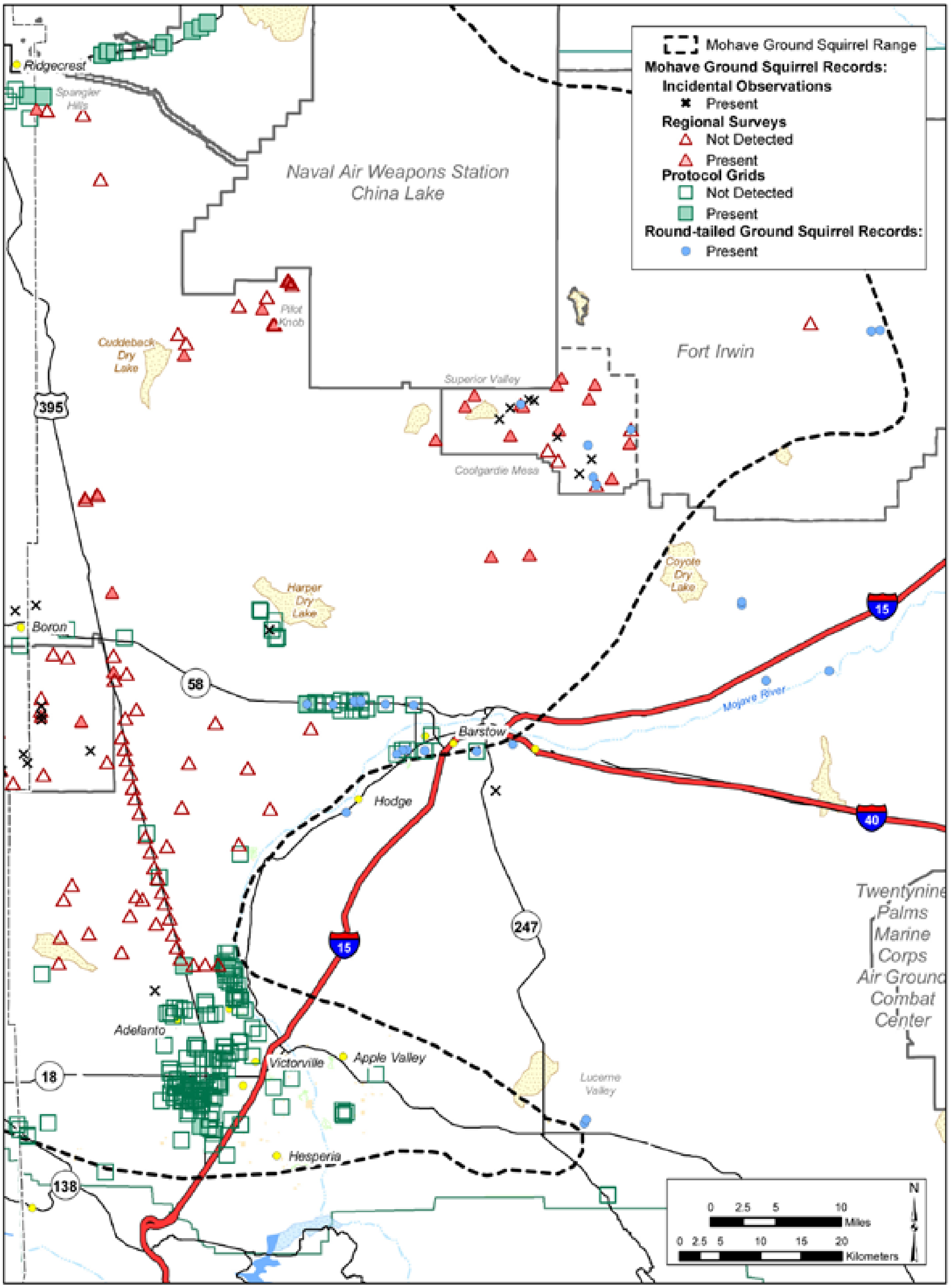

Figure 4. The contact zone between the Mohave ground squirrel and the round-tailed ground squirrel. This shows the distribution of trapping sessions conducted for regional and protocol surveys, as well as incidental observations of Mohave ground squirrels. Circles show sites where round-tailed ground squirrels have observed or captured. These data cover the period 1998-2007.

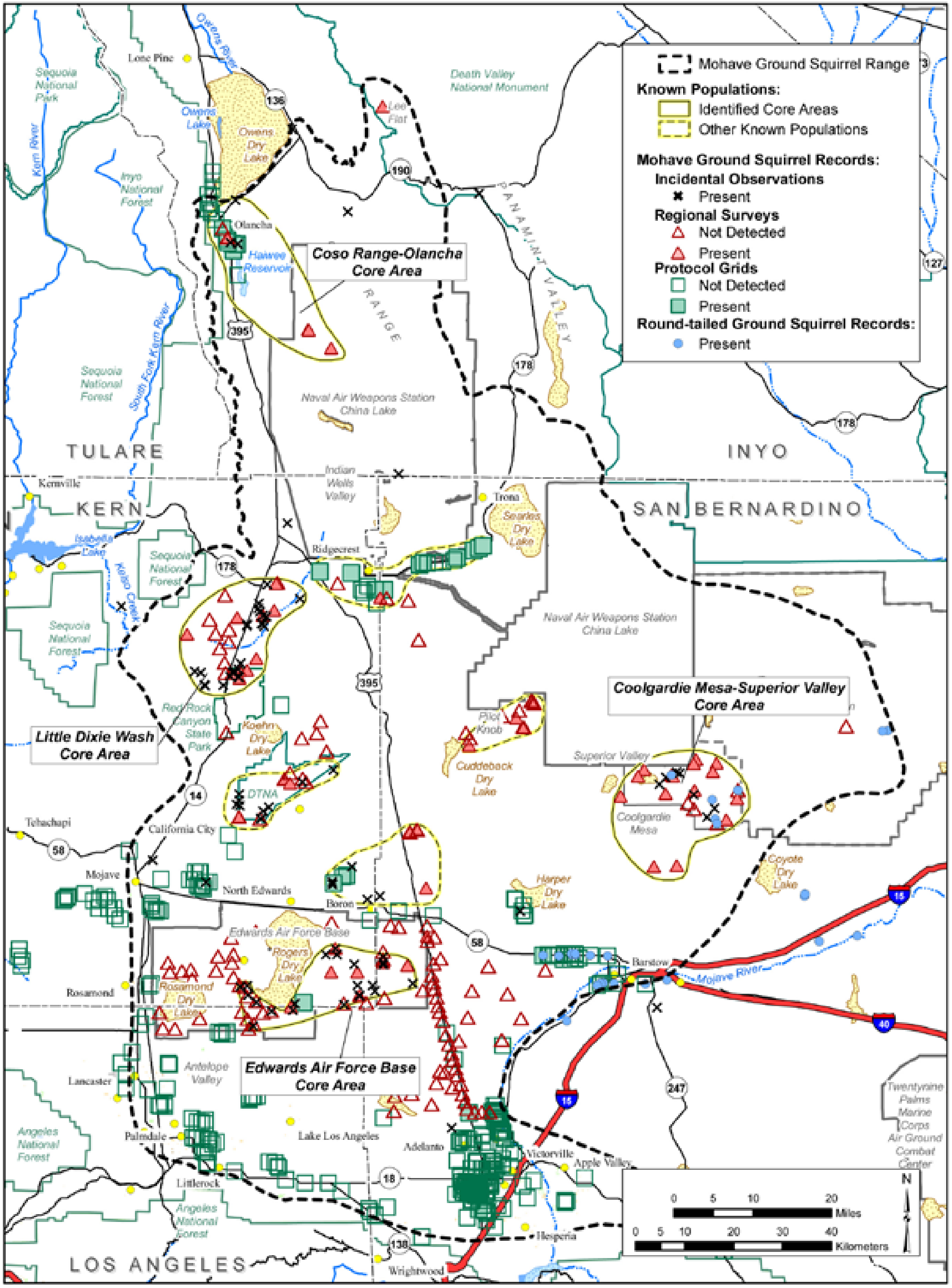

Figure 5. The geographic locations of currently known Mohave ground squirrel populations, including 4 identified core populations and 4 other populations.

exist outside the 8 areas in which recent positive records are concentrated.

The significance of negative records must be interpreted carefully as well. When regional surveys or protocol trapping fail to detect Mohave ground squirrels, it is important to keep in mind that this in itself cannot be used as evidence that the species is absent or that the area does not provide habitat for the species. There are a number of other circumstances that could result in lack of captures, such as locating a trapping grid in a small patch of marginal or unsuitable habitat, abundance of natural foods that reduce the attractiveness of the bait, low population density due to a series of dry years, or trapping early in the season before juveniles begin their dispersal movements. If trapping grids are not randomly sited, it is not valid to infer from a lack of captures at the grid sites that Mohave ground squirrels are absent in the surrounding habitat. Any conclusions would apply only to the grid sites themselves. In general, the most that can be concluded from lack of captures is that the negative results provide no evidence that the species is present. However, if repeated trapping efforts over a period of several years fail to detect Mohave ground squirrels, it becomes more and more probable that the species is very rare, if not absent, from the study area.

The distribution of trapping effort among private, military, and public land ownerships has been distinctly uneven over the past 10 years. Almost all protocol trapping surveys have been conducted on private lands or on highway rights-of-way, because of the regulatory requirement to determine presence or absence of the Mohave ground squirrel on proposed project sites. Military lands make up about 37% of the land surface within the range boundaries, but have been the locations for only 7.4% of all trapping records (Table 2). While Edwards Air Force Base and the Western Expansion Area of Fort Irwin have been sampled intensively, very little trapping effort has been expended on the remainder of Fort Irwin or on China Lake NAWS.

Core Areas

Data collected over the past 10 years has made it possible to identify 4 areas within the range of the Mohave ground squirrel that still support relatively abundant and widespread populations. These core areas are defined by 3 criteria. First, there must be evidence that Mohave ground squirrel populations have persisted for a substantial period of time, on the order of 2-3 decades. Second, the species must be currently found at a minimum of 6 locations throughout the area. Third, the total number of individuals detected since 1998 must be $\geq$30. The 4 areas that are currently known to satisfy these criteria are Coso/Olancha, Little Dixie Wash, Coolgardie Mesa/Superior Valley, and Edwards Air Force Base (Fig. 5). These 4 core areas total about 1,672 km^2, or about 8.4% of the entire historic range (Table 3). During the period 1998-2007, there have been 135 positive records in core areas, accounting for 68.2% of the total 198 positive records. It is important to emphasize that these identified core areas are simply the only important population centers that have been identified thus far. There are very likely to be other core areas in parts of the geographic range that have not been adequately sampled in the last 10 years.

Coso/Olancha Core Area.—China Lake NAWS sponsored field studies of the Coso Hot Springs area

Table 2. An analysis of trapping effort on military lands within the range of the Mohave ground squirrel (MGS) during the period 1998-2007. The number of sites refers to the number of distinct trapping grid locations, while the number of records is the total number of trapping sessions at all sites, regardless of whether Mohave ground squirrels were captured.

Military Base	Area (km^2)	% MGS Range	No. Sites	No. Records	% Records
China Lake NAWS	4400	22%	2	20	1.8%
Fort Irwin	1800	9%	18	19	1.7%
Edwards AFB	1200	6%	43	43	3.9%
Totals	7400	37%	63	82	7.4%

in 1978 that detected 35 Mohave ground squirrels at a number of sites through trapping and visual observations (Zembal and Gall 1980). In the following year, trapping was carried out at 8 sites throughout the Coso Range and in Rose Valley to the west (Leitner 1980). A total of 124 individual Mohave ground squirrels were captured at 7 of the 8 trapping grids. A monitoring program in the Coso Range and Rose Valley from 1988 through 1996 resulted in the capture of over 1400 juvenile and adult Mohave ground squirrels (Leitner and Leitner 1998). Aardahl and Roush (1985) failed to trap the species at a site near Olancha in 1980, but did observe several individuals in the same general area.

During each of the past 7 years (2001-2007), Mohave ground squirrels have been trapped at 2 permanent grids in the Coso Range (Leitner 2001, 2006, 2008). A total of 89 adults have been captured over this period. The species has also been detected regularly in the Olancha area, where 29 adult captures were recorded at 5 sites from 2002 to 2005. The Coso/Olancha area clearly qualifies as an important core area, based upon the persistence of Mohave ground squirrel populations here for 30 years, the presence of the species at many sites, and the number of animals detected.

Little Dixie Wash Core Area.—Mohave ground squirrels were first recorded in the Little Dixie Wash region in 1931 and 1932, when specimens were collected at Freeman Junction and on the east side of Walker Pass (CNDDB Occ. #21 and #52). Trapping surveys by the BLM in 1974 and 1975 resulted in 17 captures at 7 localities in Dove Springs Canyon and Bird Spring Canyon (CNDDB Occ. #84, #174, #175, and #191-194). Aardahl and Roush (1985) reported capturing a total of 94 individuals (both adults and juveniles) at 6 grids in the Little Dixie Wash area from April-July 1980. Finally, trapping at 2 sites in 1994 yielded a total of 12 Mohave ground squirrels (Scarry et al. 1996). Additional occurrences were documented at 10 other locations in this region during the period 1974-1990. Thus, Mohave ground squirrels were recorded at 27 locations in the Little Dixie Wash area from 1931 through 1996.

Recent field studies have been conducted in the Little Dixie Wash area during the period 2002-2007. In 2002, a total of 19 adult Mohave ground squirrels were captured at 6 of 7 grid locations (Leitner 2008). This was followed by more intensive studies at the Freeman Gulch site, with a total of 108 adults and 101 juveniles recorded from 2003 through 2007. Pit-fall trapping for reptiles in the Dove Springs Open Area resulted in the incidental capture of 6 Mohave ground squirrels at 4 different locations. Finally, a trapping survey in 2007 yielded 7 adults at 4 grids near the northern boundary of Red Rock Canyon State Park (Leitner 2008). The Little Dixie Wash core area has supported Mohave ground squirrel populations for over 70 years and recent records confirm that the species is abundant and widespread here.

Coolgardie Mesa/Superior Valley Core Area.— Mohave ground squirrels were first discovered in 1977 north of Barstow on the plateau that stretches from Coolgardie Mesa north to Superior Valley (Wessman 1977). The species was detected at 9 locations, with 1-3 individuals reported at each site. In 1980, Aardahl and Roush (1985) trapped 2 grids in Superior Valley, capturing 24 individuals (both adults and juveniles). A total of 24 Mohave ground squirrels were subsequently recorded at 5 sites in 1981 and 1982 (CNDDB Occ. #206-210). In 1994, 4 individuals were captured at 2 trapping grids in this area (Scarry et al. 1996).

Two recent surveys have been carried out in the Coolgardie Mesa/Superior Valley area. Trapping at 4 sites in 2002 yielded Mohave ground squirrel captures at each location for a total of 14 adults. A more extensive survey of the Western Expansion Area of Fort Irwin in 2006 and 2007 resulted in 36 individuals captured at 10 of 12 trapping grids. There is clear evidence that Mohave ground squirrels have persisted here for at

Table 3. The estimated sizes of the 4 identified core areas, as measured in square kilometers and in acres. The number of positive Mohave ground squirrel records for the period 1998-2007 is given for each core area.

Core Area Name	Area (km^2)	Area (acres)	Number of Positive Records
Coso / Olancha	452	111,690	33
Little Dixie Wash	393	97,172	44
Coolgardie Mesa / Superior Valley	516	127,450	23
Edwards Air Force Base	311	76,761	35

least 30 years. Recent surveys have documented that the species was present at 14 of 16 trapping sites and in several cases a substantial number of individuals was captured. This core area is at the eastern edge of the range and several captures or observations of animals that appear to be round-tailed ground squirrels have been recorded here. The potential for hybridization in this area between these 2 closely related species should be carefully investigated.

Edwards Air Force Base Core Area.—A number of surveys have documented the past occurrence of Mohave ground squirrels on Edwards Air Force Base, with most records located to the north, east, and south of Rogers Dry Lake. The earliest observations were made during the period 1973-1977 in the area south of Rogers Dry Lake (CNDDB Occ. #265). Seventeen Mohave ground squirrels were trapped in 1988 at 3 sites northeast of Rogers Dry Lake (ERC Environmental and Energy Services Company 1989). Additional trapping in 1993 in this same area resulted in captures of many adults and juveniles (Deal et al. 1993, Mitchell et al. 1993). Surveys at Mt. Mesa to the southeast of Rogers Dry Lake yielded 9 Mohave ground squirrels in 1992 (U.S. Fish & Wildlife Service 1993) and over 30 individuals in 1993 (Deal et al. 1993, Mitchell et al. 1993). A total of 13 Mohave ground squirrels were trapped in 1994 at 4 sites in halophytic saltbush scrub to the south and southwest of Rogers Dry Lake (Buescher et al. 1995). The species was recorded at 4 additional locations to the east of Rogers Dry Lake during the period 1981-1991.

Recent field studies have clearly delineated a core area on Edwards Air Force Base, with all Mohave ground squirrel records since 2000 localized to the east and south of Rogers Dry Lake. Trapping surveys were conducted at 19 grids in this area during the period 2000-2005, with a total of 29 adults and 4 juveniles captured at 8 of the study sites (Vanherweg 2000, Leitner 2003, Air Force Field Test Center 2004 and 2005, Leitner 2008). Although no captures were recorded at the 8 grids south of Rogers Dry Lake in 2005, Mohave ground squirrels are known to be present here, based upon 6 incidental observations. Mohave ground squirrel populations have been known in this core area for over 30 years and the large numbers of recent records demonstrate that the species is still well-distributed here. To date, this is the only core area known to exist in the southern part of the range.

Connectivity between Core Areas

The 4 core areas are isolated from each other by distances ranging from 48-80 km. It will be an important conservation goal to ensure sufficient connectivity between them to allow gene flow. Figure 6 shows the locations of the core areas with possible habitat corridors illustrated.

The potential corridor between the Coso/Olancha core area and Little Dixie Wash follows a narrow strip of public land between the Sierra escarpment and the boundary of China Lake NAWS. It is not clear that this corridor is effective because of its minimal width (1-4 km) and because there is no firm evidence that it is currently occupied. There may well be an alternative corridor through China Lake NAWS, but the U.S. Navy cannot guarantee permanent protection and, again, there is no proof that continuous Mohave ground squirrel populations exist here.

Connectivity between the Little Dixie Wash core area and Edwards Air Force Base is most likely to be achieved by protection of a north-south habitat corridor along US Highway 395. This linkage appears to provide the highest quality habitat connection between these 2 core areas. It would also help to provide connectivity among other known populations in the Ridgecrest area, the DTNA, Pilot Knob, and the Boron region. There are no recent Mohave ground squirrel records along much of this corridor, so it is not clear that it is currently occupied.

The most effective corridor linking the Coolgardie Mesa/Superior Valley core area with other populations is probably thorough the Pilot Knob region. This connection is relatively short and crosses apparently good quality habitat. Although the most direct route is across a corner of the China Lake NAWS, public lands just to the south could also provide connectivity. An alternative linkage would be to the southwest toward Edwards Air Force Base across the broad valley centered on Harper Dry Lake. However, this route is lower in elevation, receives less rainfall, and habitat here is of lesser quality.

The lack of data concerning the existence or status of Mohave ground squirrel populations in these potential corridors is a serious problem. While these routes may seem geographically appropriate in providing linkages between populations, it will be important to conduct field studies to determine whether or not they are actually occupied.

MANAGEMENT RECOMMENDATIONS

The database of Mohave ground squirrel records that has been assembled for this analysis should be maintained by CDFG or another suitable public agency and made available for on-line access by interested researchers, agency staff, consultants, and conservation organizations. An interactive mapping system should be developed in conjunction with the database, so that

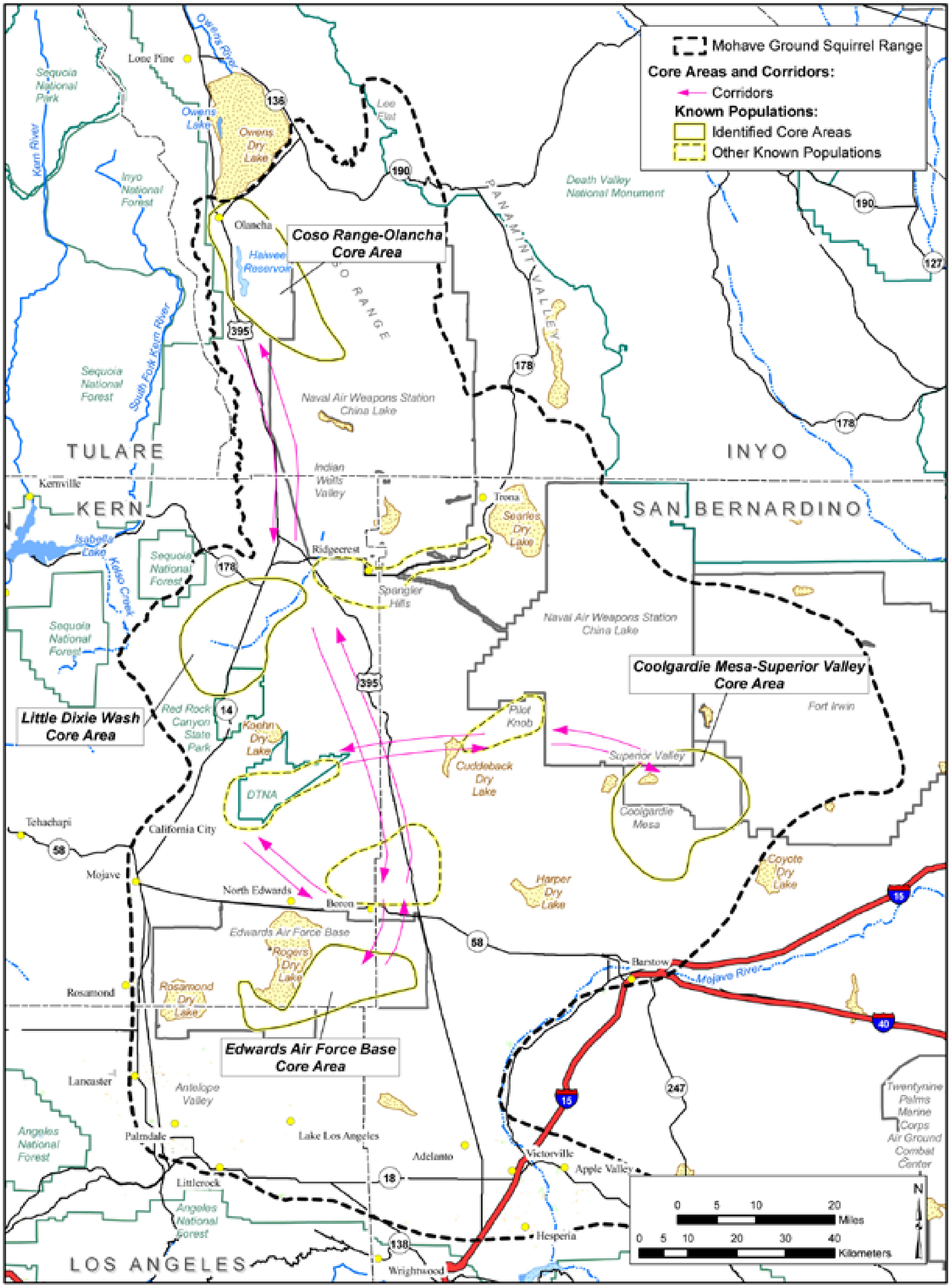

Figure 6. Map of potential habitat corridors that may provide connectivity between identified core areas and other known Mohave ground squirrel populations.

users could obtain map displays of areas of interest. As recommended by Brooks and Matchett (2002), a system should be developed to collect both positive and negative data on a continuing basis from biologists, agency staff, and consultants. It would be desirable to issue an annual report with appropriate maps to provide updated information on Mohave ground squirrel occurrences.

It is clear that additional field surveys are urgently needed to provide a more comprehensive picture of Mohave ground squirrel occurrence and status throughout its range. It is also clear that surveys to date have been seriously inadequate in documenting patterns of Mohave ground squirrel distribution because trapping sites have for the most part not been selected according to a randomized scheme. In the absence of a randomized sampling procedure, the results of such surveys apply only to the trapping site and cannot be extrapolated to the general region. It is recommended that a range-wide survey be conducted, with sampling locations determined on a randomized basis. Since this would be an expensive and logistically difficult undertaking, it may be more realistic to develop a survey plan that could be implemented gradually over several years as funding becomes available. The first step could be to establish a sampling frame covering the entire Mohave ground squirrel range, with the area divided into sampling units, perhaps 10 x 10 km or smaller. When a survey is planned for a particular region, trapping grids could be sited in sampling units chosen at random. This system would be quite flexible, since it could be implemented at different scales as appropriate for the purposes of the sponsoring organization. It is recommended that the Mohave Ground Squirrel Technical Advisory Group develop such a range-wide randomized sampling plan and submit it to the CDFG, BLM, and military installations for consideration.

It appears to be of critical importance to acquire more data concerning the status of the species in the northern and central parts of its range (Fig. 7). Surveys should be carried out on both the north and south ranges of China Lake NAWS, on Fort Irwin, and along the corridor north from EAFB to Ridgecrest. There has

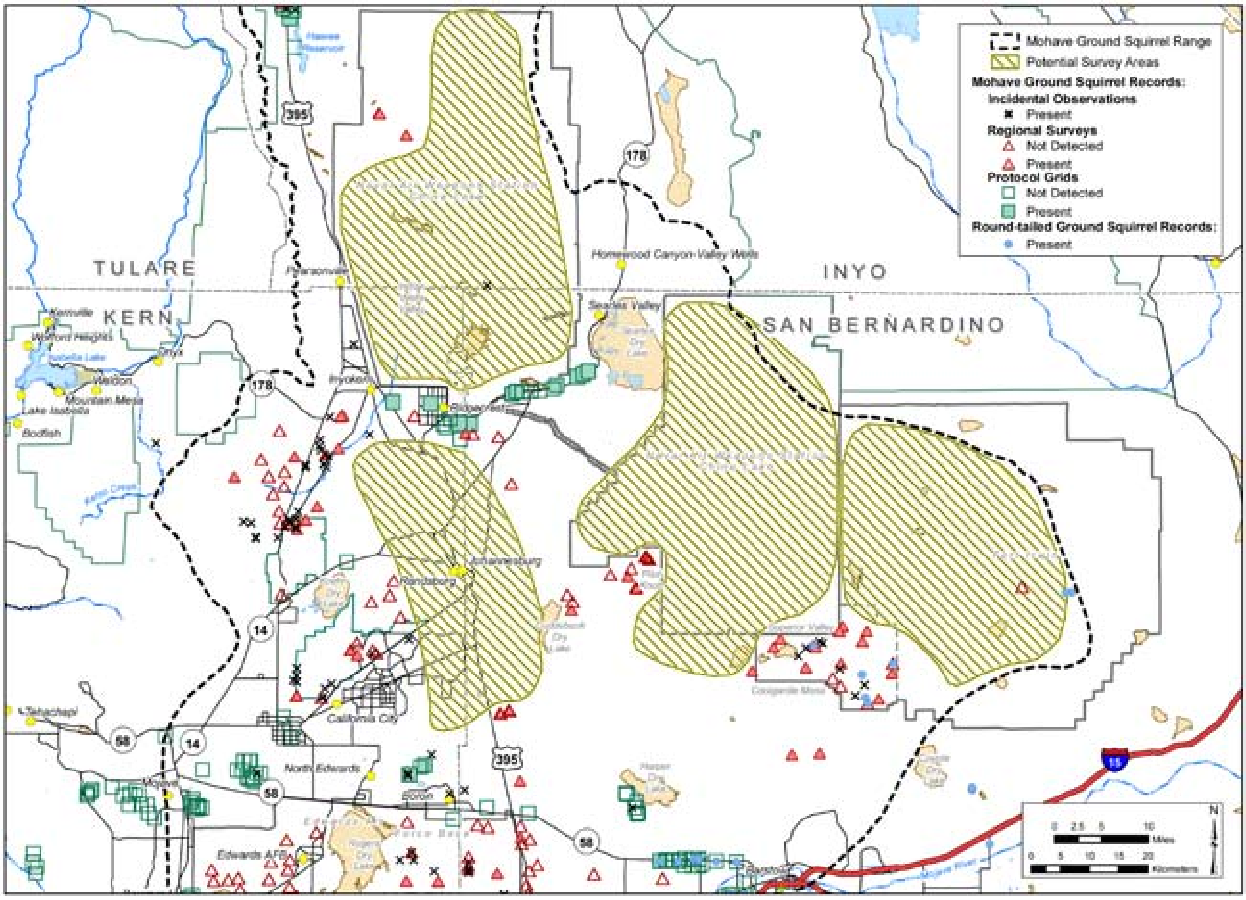

Figure 7. Potential survey areas in the northern and central portions of the Mohave ground squirrel range, showing their geographic relationship to survey efforts during the period 1998-2007.

been little or no sampling during the period 1998-2007 in these 4 extensive areas. A careful study plan should be developed to ensure adequate survey coverage within each area.

It is also recommended that field surveys be conducted in key areas within the southern range of the species in order to determine whether viable populations still remain outside of EAFB (Fig. 8). The trapping surveys could focus on public lands, but a serious attempt should be made to obtain permission for surveys on private lands as well. Because of the pace of development within the southern portion of the Mohave ground squirrel range, this exploratory work needs to be carried out with urgency.

The region southwest of the town of Mojave was identified in the West Mojave Plan (BLM 2003) as the Kern County Study Area. The West Mojave Plan recommended that Mohave ground squirrel trapping surveys be conducted here on public lands. The possibility was left open that the boundary of the Mohave Ground Squirrel Conservation Area could be modified to include these public lands if justified by survey results. A number of protocol trapping surveys have recently been carried out on private land in this area in connection with proposed wind energy projects. Although no Mohave ground squirrels have been trapped thus far, there have been 2 reported visual detections. It is recommended that additional trapping surveys be authorized on both public and private property, especially in areas that have not yet been investigated.

More information is needed about the relationship between the Mohave ground squirrel and its sibling species, the round-tailed ground squirrel. There are recent reports of round-tailed ground squirrel occurrences well inside the historic Mohave ground squirrel range to the west of Barstow and in the Western Expansion Area of Fort Irwin. Round-tailed ground squirrels seem well-adapted to land disturbance in agricultural areas and on the outskirts of towns. It is possible that hybridization is occurring where the 2 species come in contact. It is

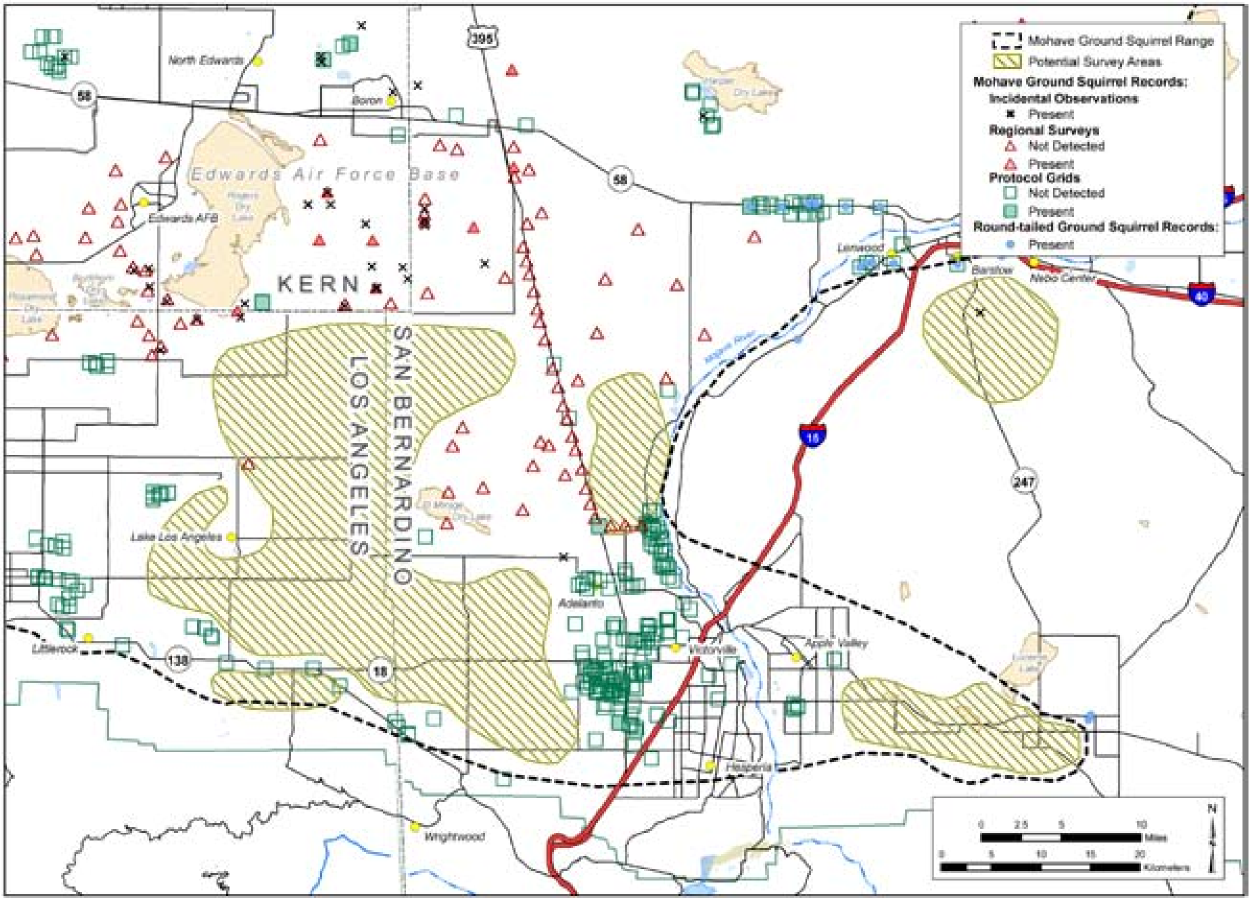

Figure 8. Potential survey areas in the southern portion of the Mohave ground squirrel range, showing their geographic relationship to survey efforts during the period 1998-2007.

recommended that surveys be carried out to determine the current eastern limits of the Mohave ground squirrel range and establish a baseline so that future westward movement of round-tailed ground squirrels could be detected. It is also recommended that genetic studies be undertaken in the contact zone to investigate the extent of hybridization where the 2 species co-occur.

Although trapping is the most effective method of identifying areas that support Mohave ground squirrel populations, it is recommended that certain modifications of current trapping procedures be tested. Trained wildlife dogs could be used to screen large areas and help focus trapping efforts on the most promising sites. Most trapping efforts to date have used large 100-trap grids. It would be of interest to try other trap configurations, such as more numerous small grids (for example, arrays of 20 traps) and long (>1000 meter) linear transects. Finally, such alternative trap configurations could be used in combination with adaptive cluster sampling (Thompson et al. 1998), which would allow for increased effort adjacent to a sampling unit where a Mohave ground squirrel is detected.

It is essential to protect BLM lands within the Mohave Ground Squirrel Conservation Area by enforcing the 1% limitation on ground disturbance (Fig. 1) called for under the West Mojave Plan (BLM 2005). In addition, acquisition of private lands that are included within the boundaries of the Conservation Area should be pursued aggressively, especially land that is included within known core areas. Finally, there may be important Mohave ground squirrel populations outside the Conservation Area that could protected by acquisition of private lands and careful management of BLM lands. The area stretching from the DTNA southeast toward Boron may be a good example of such a conservation opportunity.

ACKNOWLEDGMENTS

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APPENDIX 1

UNPUBLISHED REPORTS OF REGIONAL TRAPPING STUDIES CONDUCTED DURING THE PERIOD 1998-2007

Air Force Flight Test Center. 2004. Inventory for Presence of Mohave Ground Squirrel at Edwards Air Force Base, California. 26 pp. + appendices.

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The University of Notre Dame

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Fire and Changes in Creosote Bush Scrub of the Western Sonoran Desert, California

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ABSTRACT: Seven years of above normal precipitation between 1976 and 1983 encouraged heavy growth of native annuals and exotic grasses in the western Sonoran Desert. Unprecedented fires in creosote bush scrub started mostly after 1978. Analysis of several burns near Palm Springs revealed that most shrubs, including *Larrrea tridentata, Ambrosia dumosa* and *Opuntia* spp., are poorly adapted to relatively low intensity fires as evidenced by limited sprouting and reproduction. These shrubs were replaced by open stands of *Encelia farinosa*, native ephemerals, and European exotics, mostly *Bromus rubens* and *Schismus barbatus*. The rapid selective thinning of creosote bush scrub species suggests that the modern biogeography of this ecosystem may be controlled, in part, by recurrent burning.

INTRODUCTION

Fires are infrequent in the Sonoran Desert owing to limited biomass, wide spacing between shrubs and sparse ground cover (Humphrey, 1949, 1962). Recent studies in Arizona (Rogers and Steele, 1980) and California (Tratz and Vogl, 1977: Tratz, 1978; O'Leary and Minnich, 1981) indicate that many desert perennials are poorly adapted to burning. Successional studies in creosote bush scrub reveal postdisturbance recolonization by long-lived species is very slow initially and may require hundreds of years (Vasek, 1980, 1983). Thus rare fires may have long-term impact on the structure and composition of this community.

Heavy growth of native and exotic annual vegetation promoted by extraordinarily heavy precipitation between 1976 and 1983 resulted in unprecedented fires in creosote bush scrub vegetation along the western margins of the Mojave and Sonoran deserts of southern California. This study documents fire and early postfire succession in creosote bush scrub in several burns near Palm Springs, and it evaluates the stability and biogeography of this ecosystem in relation to recurrent fire.

STUDY AREA

Four sites on Quaternary alluvial fans descending from the E scarp of the San Jacinto Mountains at the end of the Coachella Valley near Palm Springs, California, were chosen for study (Fig. 1). Coarse-textured soils are well-drained, moderately alkaline with a minimum of organic matter (Fraser, 1931; Proctor, 1968; Knecht, 1980).

The climate of the Coachella Valley is extremely arid owing to its subtropical latitude and to rain shadows of the San Jacinto Mountains (Bailey, 1966). Average annual rainfall at Palm Springs, mostly from winter cyclonic storms, is 138 mm (Table 1). Summers are hot and dry, although tropical moisture from the equatorial Pacific produce occasional thunderstorms, mostly over the nearby mountains.

VEGETATION

Most of the Sonoran Desert is covered with creosote bush scrub consisting of scattered low shrubs less than 2 m. Representative growth forms include evergreen

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sclerophyllous and deciduous shrubs, subligneous subshrubs, leaf and stem succulents, and annual herbs (Johnson, 1974; Burk, 1977). Bajadas and adjacent mountainsides in the Coachella Valley are covered by *Larrea tridentata*, *Encelia farinosa*, *Hilaria rigida*, *Enchinocereus engelmannii*, and *Krameria grayi*. Vegetation on the plains and lower bajadas, including the study sites, is dominated by *L. tridentata*, *Ambrosia dumosa* and *E. farinosa*, which may form 60-100% of total vegetation cover (McHargue, 1973; Shreve and Wiggins, 1964). *Cercidium floridum*, *Olynea tesota*, *Dalea spinosa*, *Beloperone californica* and *Hyptis emoryi* are common along washes. Succulents such as *Ferocactus acanthodes*, *Echinocereus engelmannii*, *Opuntia basilaris*, *O. bigelovii* and *O. echinocarpa* reach maximum densities on sandy hillsides and bajadas with rocky, gravelly, or sandy substrates (McHargue, 1973).

FIRE HISTORY

Until the last decade, burning was almost unknown in the area (Fig. 1). Two large fires in 1911 and 1945 burned chaparral and mixed evergreen forests above 1200 m. A 3600-ha fire on the N slope of Mt. San Jacinto in 1973 spread into a small area of creosote bush scrub (O'Leary and Minnich, 1981). Two rare Mexican west coast tropical storms (September 1976, August 1977), followed by abnormally stormy winters from 1977-1978 to 1979-1980 and 1982-1983, caused sustained above-normal precipitation

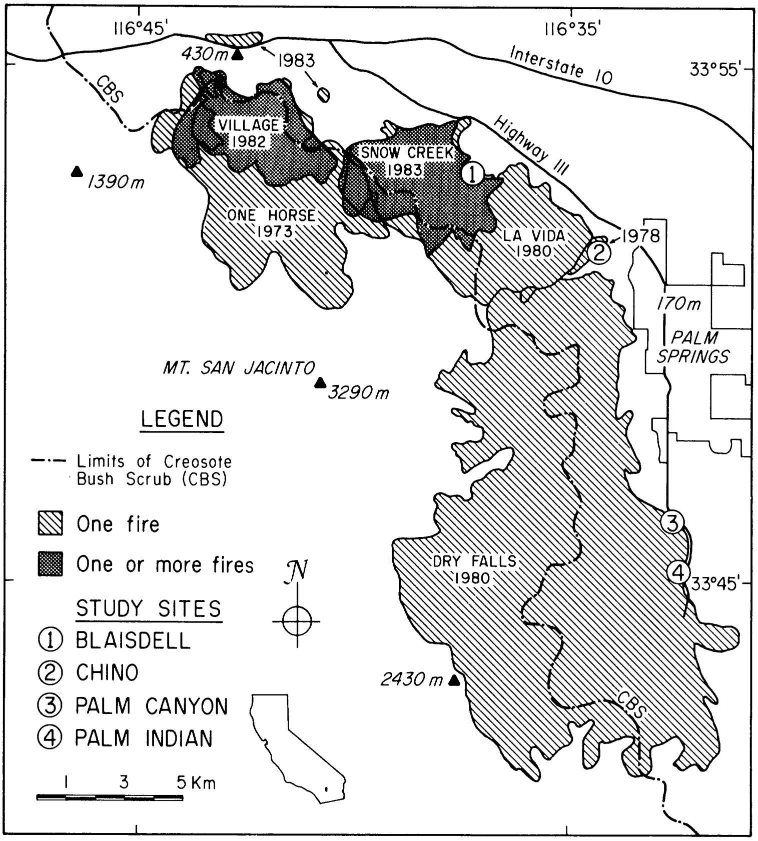

Fig. 1.—The study sites and fire perimeters. Limits of cresote bush scrub are interpreted from 1:30,000 scale aerial photography (1971) on file at the Department of Earth Sciences, University of California, Riverside

(Table 1) which encouraged heavy growth of shrubs and herbaceous understory. Beginning in 1978, a series of fires spread through dried herbaceous fuels into extensive areas of creosote bush scrub, including the Chino Canyon fan (500 ha, 1978), Blaisdell and Chino canyons (2800 ha, 1980), and the E scarp and alluvial fans below 1300 m from Chino Canyon S to Palm Canyon (6000 ha, 1980). A 1200-ha burn in 1982 overlapped large areas burned in 1973 near Snow Creek. In 1983, the first of three fires reburned portions of Snow Creek and Blaisdell Canyon. Two smaller fires also occurred along Snow Creek road and Interstate 10.

The fires in creosote bush scrub characteristically spread during periods when ambient temperatures averaged 35-40 C and relative humidity ranged from 10-25%. High winds (10-20 ms^{-1}) were caused by the typical spring and early summer gravity acceleration of descending coastal marine air spilling through San Gorgonio Pass. Upcanyon winds and nocturnal air drainage promoted fire spread on the eastern face of Mt. San Jacinto. The flames reduced the herb layer to a low stubble, indicative of fast-moving, low-intensity fires.

SITE SELECTION AND METHODS

Four sites were located on relatively homogeneous terrain (*i.e.*, avoiding large washes or rock outcrops) at the fire boundaries on the Chino, Blaisdell and Palm Canyon alluvial fans in order to compare burned vegetation with adjacent unburned stands (Fig. 1). The areas were surveyed between 25 April and 27 May 1983, when desert annuals were declining and perennials were in full growth or flower.

Perennial and annual plants were analyzed separately, with major emphasis placed on perennial cover and density. In unburned transects, the vegetation sampled is assumed to represent the prefire state of burned areas. In each site, two 100-m parallel transects were employed in burned and unburned areas (200 m for each). Both belt and line methods of sampling were used along each 100-m transect (Mueller-Dombois, 1974). The line intercept method was used to obtain percent cover (intercept distance) and density of perennial species (*cf.* Canfield, 1942). Each plant along the intercept was measured, identified and counted. Seedlings on each intercept were counted as part of total perennial cover, and were also noted separately. Belt transects (100 m x 1 m) were used to determine seedling density. Seedlings were counted and time of establishment was assigned as first postfire growing season (older plants > 5 cm height) or later growing season (< 5 cm). A 1-m-sq area was located at the end point of each transect to estimate herbaceous cover and floristic composition.

In transects within the burns, surviving plants, sprouting behavior and mortality (fire-killed snags) were recorded. Fire damage was estimated by qualitatively ranking plants as burned, scorched or green. Burned plants showed pyrolysis of foliage and fine

TABLE 1.—Annual precipitation at Palm Springs (source: California 1984)

Season	Total (mm)	Percent of normal
1889-1983 Mean	138	
1976-1977	174	126
1977-1978	289	209
1978-1979	188	136
1979-1980	412	299
1980-1981	64	46
1981-1982	98	71
1982-1983	222	161

stems, leaving a stump or main stems. Scorched plants retained all or most branches and dried foliage. Green plants retained living foliage or escaped fire entirely. In belt transects, plant snags were counted and ranked for fire damage and recovery. Seedlings were counted in each meter and assigned establishment dates as in unburned areas.

RESULTS

The vegetation was sampled 3 growing seasons after burns at Blaisdell, Palm Canyon and Palm Indian sites and after 5-growing seasons at the Chino site. However, data for Chino were merged with other data because there was insufficient data from the single 1978 site to extrapolate small differences in succession from species composition which may be more related to site than temporal changes associated with age class. Nineteen perennial and 10 herb species were recorded.

UNBURNED VEGETATION

Unburned perennial cover averaged 21% and was dominated by *Larrea tridentata*, *Ambrosia dumosa*, and *Encelia farinosa* (Table 2). Wash species (*Acacia greggii*, *Beloperone californica*, *Hyptis emoryi*) and cacti (*Opuntia acanthocarpa*, *O. bigelovii*) were occasional in all sites. Native herb cover (*Aristida adscensionis*, *Chaenactis fremontii* and *Chorizanthe brevicornu*) varied greatly while the European exotics, *Bromus rubens* and *Schismus barbatus*, were nearly everywhere (Fig. 2).

BURNED VEGETATION

Fire damage to perennials.—Most perennials were scorched, although the majority of shrubs were locally burned in several sites, particularly the Blaisdell fan. The pattern of shrub damage was species-specific, suggesting that the combustion of shrubs was more influenced by individual species morphology and fuel properties than spatial variations in fire behavior (Table 3). *Larrea tridentata* was typically only scorched despite its resinous foliage and the dense herbaceous cover growing in organically rich eolian sedimentary mounds beneath. Most main stems were unburned and often contained green foliage. Flame heights from herbaceous fuels were apparently insufficient to burn *L. tridentata* canopies owing to limited herbaceous fuels, limited foliar dead fuel content, and spreading branch habit (low fuel continuity). *Encelia farinosa* was mostly scorched due to the morphology of pencil-thick branches which support an umbrella of leaves with few stems beneath. Only leaves and branches near the ground burned, leaving foliage on ultimate stems. *Ambrosia dumosa* regularly burned because the canopy comprises numerous small branches with a finely divided branching pattern close to herbaceous fuels which maximizes fuel continuity, surface to volume ratio and rapid pyrolysis.

The cacti, including *Opuntia acanthocarpa*, *O. bigelovii*, and *Ferocactus acanthodes*, were normally scorched. The dense spines of *O. bigelovii* tended to carry flames up the crown. *Beloperone californica* and *Hyptis emoryi* were usually less damaged than other shrubs, perhaps owing to higher fuel moisture content in wash habitats. *Hyptis emoryi* is characterized by an upward branching habit, and its upper stems extended above flames. Among infrequent shrubs (data not shown), *Acacia greggii* and *Dalea californica* rarely burned because of their arboreal and semideciduous growth habits. *Bebbia juncea*, *Ephedra californica* and *Krameria grayi* normally burned due to their low growth habits and compact crowns.

Sprouting and mortality. Sprouting of most perennials was limited and depended upon local fire intensity. At the heavily burned Blaisdell site, for example, most plants were reduced to ash and mortality was nearly universal; sprouting was intermittent among scorched shrubs at the other sites (Table 3).

Burned shrubs of most species sprouted less than scorched ones. *Larrea tridentata*, *Ambrosia dumosa* and *Encelia farinosa* rarely sprouted even among scorched individuals that retained full canopy foliage. Many *L. tridentata* shrubs with living foliage after burning died later, presumably as a result of basal cambium damage. Scattered resprouts of *Opuntia acanthocarpa*, *O. bigelovii*, *Echinocereus engelmannii* and *Ferocactus acanthodes*

TABLE 2.—Density (D) and cover (C) of established (unburned) and resprouting (burned) shrubs. Density is expressed in number of plants per 100 m^2, cover in percent ground covered

	Blaisdell				Chino				Palm Canyon				Palm Indian			
	Unburned		Burned		Unburned		Burned		Unburned		Burned		Unburned		Burned	
Species	D	C	D	C	D	C	D	C	D	C	D	C		C	D	C
Larrea tridentata	2.5	3.1	0	0	3.5	3.4	0	0	3.0	4.2	0	0	8.0	13.4	0	0
Ambrosia dumosa	20.0	13.0	0	0	8.0	4.1	0	0	6.0	4.1	1.5	3.3	5.5	1.7	.5	.2
Encelia farinosa	1.0	.9	0	0	11.5	9.2	1.5	2.0	13.0	10.6	2.0	2.6	3.0	1.4	2.5	3.5
Opuntia acanthocarpa	3.0	1.2	0	0					3.0	1.7	1.0	.3	1.0	.2	0	0
O. bigelovii													7.5	1.2	2.0	.5
Hyptis emoryi					0	0	1.0	.8	2.5	3.0	1.0	.7	1.5	1.6	1.0	.6
Krameria grayi	2.5	1.5	0	0	.5	.3	0	0								
Dalea californica	1.0	.4	0	0												
Mirabilis bigelovii	.5	.3	0	0												
Beloperone californica					3.5	2.0	7.0	3.7								
Hilaria rigida					1.0	.5	0	0								
Ferocactus acanthodes					.5	.1	0	0								
Acacia greggii									0	0	.5	1.4				
Bebbia juncea													.5	.9	.5	.6
Echinocereus engelmannii													.5	.1	0	0
Total	30.5	20.4	0	0	28.5	19.6	9.5	6.5	27.5	23.6	6.0	8.3	27.5	20.5	6.5	5.4

were surrounded by numerous skeletons of dead individuals. The wash species *Beloperone californica* and *Hyptis emoryi* exhibited well-developed stump and crown sprouting. *Acacia greggii* resprouted to former canopy cover within 3 years.

SEEDLING ESTABLISHMENT

More shrub seedlings established on burned than on unburned sites, although the pattern of regeneration varied with species and annual precipitation (Table 4). *Encelia farinosa* accounted for most of the seedlings observed during the first growing season, especially in burns. Most reproduction during the first growing season was composed of *Encelia farinosa*, primarily in burns. *Hilaria rigida*, *Opuntia acanthocarpa* and *Trixis californica* seedlings were observed in burns only after the first growing season (1980-1981). *Mirabilis bigelovii*, *Sphaeralcea emoryi* and *Bebbia juncea* also reproduced in burns mostly during the first growing season, but establishment persisted into later growing seasons. *Ambrosia dumosa* and *Ditaxis lanceolata* establishment increased in later growing seasons. Most

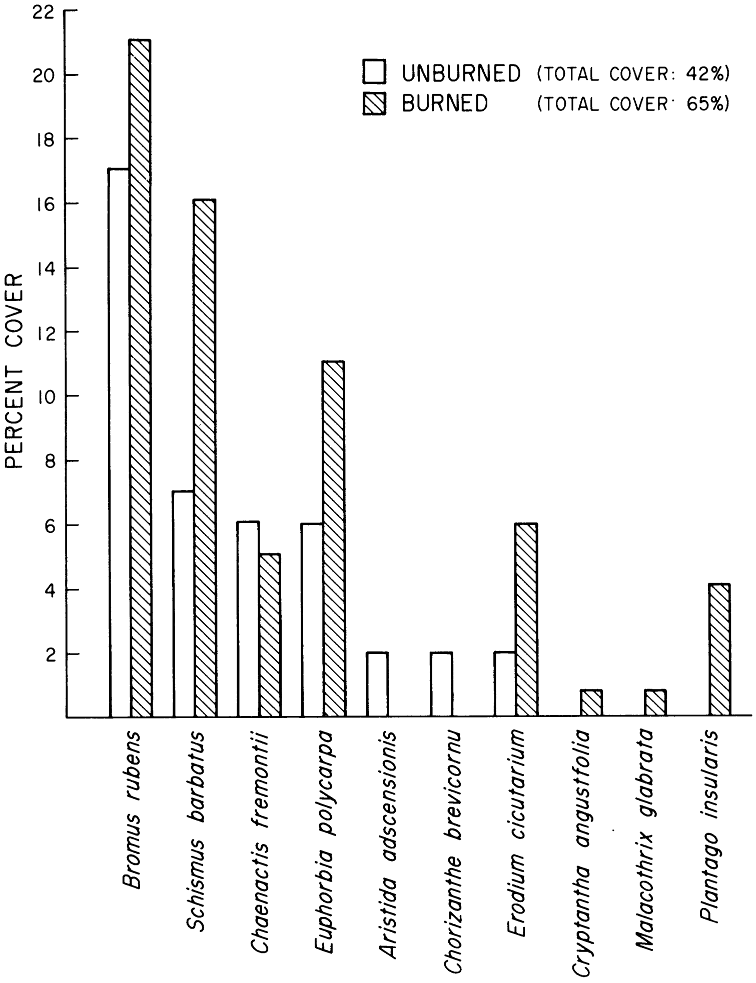

Fig. 2.—Herbaceous cover in burned and unburned sites

seedling reproduction in unburned sites was *E. farinosa* and *A. dumosa*. There was sporadic establishment of *Larrea tridentata* and *Hyptis emoryi*, mostly in unburned sites. The wet 1982-1983 season was followed by abundant reproduction of *E. farinosa* and lesser amounts of *A. dumosa* in both burned and unburned sites.

With the exception of *Encelia farinosa*, seedling densities were less than the density of established shrubs in unburned areas. Severely burned areas with few surviving perennials, such as the Blaisdell fan, had fewest seedlings (Table 2). Several infrequent perennials established no seedlings in the area, including *Acacia greggii*, *Dalea californica*, *Echinocereus engelmannii*, *Ephedra californica*, *Ferocactus acanthodes*, *Frameria grayi* and *Opuntia bigelovii* (removal of adults limited vegetative reproduction in the latter).

CHANGES IN STAND COMPOSITION

The primary effect of recent burns was the reduction of perennial cover, owing to limited sprouting combined with scarce seedling establishment of most shrubs (Fig. 3). After 3-5 growing seasons, the total cover in burned sites was about half that of unburned sites and was composed mostly of *Encelia farinosa*. The largest change was the reduction of *Larrea tridentata* because it experienced almost no sexual or asexual reproduction or resprouting.

TABLE 3.—Shrub damage, sprouting and mortality (percent)

Species	N	Burned	Resprouts	Scorched	Resprouts	Green	Resprouts	Mortality
Encelia farinosa	122	20	0	78	5	2	2	93
Ambrosia dumosa	84	81	2	16	6	3	3	89
Opuntia bigelovii	49	4	0	94	6	2	2	92
O. acanthocarpa	36	11	0	89	8	0	0	92
Larrea tridentata	35	0	0	100	3	0	0	97
Hyptis emoryi	10	0	0	100	40	0	0	60
Beloperone californica	7	0	0	100	57	0	0	43

TABLE 4.—Seedling density in initial and subsequent growing seasons

Species	Burned Area 1980-1981* growing season	Burned Area 1981-1983* growing seasons	Unburned Area 1980-1981* growing season	Unburned Area 1981-1983* growing seasons
	(number/ha)		(number/ha)	
Encelia farinosa	1460	7010	90	5650
Hyptis Emoryi	90	50	10	30
Mirabilis bigelovii	90	40	0	0
Hilaria rigida	80	0	0	0
Ambrosia dumosa	*60*	*160*	*30*	*200*
Sphaeralcea emoryi	50	10	0	0
Bebbia juncea	50	30	0	0
Beloperone californica	40	40	0	0
Opuntia acanthocarpa	30	0	0	0
Ditaxis lanceolata	10	60	0	0
Trixis californica	10	0	0	0
Larrea tridentata	0	10	0	40

*At the Chino site, the first growing season was 1978-1979. Later growing seasons are 1979-1983

Postfire herb cover averaged 23% greater in burned than unburned stands. *Malacothrix glabrata*, *Cryptantha angustifolia* and *Plantago insularis* were found only in burned areas. Most cover was of exotic European annuals *Bromus rubens* and *Schismus barbatus* (Fig. 2).

DISCUSSION

Fire mortality and postfire succession in creosote bush scrub at Palm Springs are similar to other studies in the Sonoran Desert (Rogers and Steele, 1980; O'Leary and Minnich, 1981). Sprouting behavior of *Larrea tridentata* in the Sonoran Desert was varia-

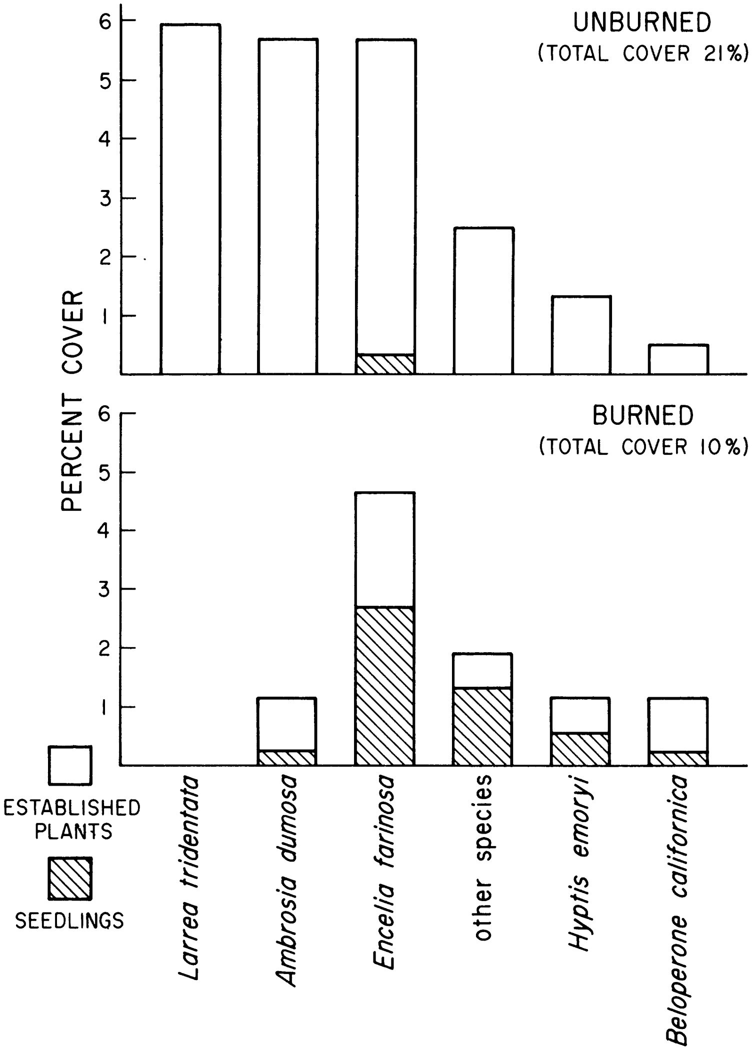

Fig. 3.—Perennial cover in burned and unburned sites (cover expressed in absolute percentages). "Other species" include *Acacia greggii*, *Bebbia juncea*, *Dalea californica*, *Echinocereous engelmannii*, *Ephedra californica*, *Ferocactus acanthodes*, *Hilaria rigida*, *Krameria grayi*, *Opuntia acanthocarpa* and *O. bigelovii*, *Ditaxis lanceolata*, *Mirabilis bigelovii*, *Spheralcea emoryi* and *trixis californica*

ble, depending primarily on fire intensity and season. Dalton (1962) found that slightly to moderately burned *L. tridentata* near Tucson, Arizona, experienced 60-70% mortality. Rogers and Steele (1980) observed minimal resprouting of *L. tridentata*. However, fire intensity and season were not reported. White (1968) found that *L. tridentata* mortality was related to season of burning, with highest mortality prior to the onset of the summer precipitation season. Increased fire intensity and duration also resulted in decreased sprout production.

At Palm Springs, sprouting of *Larrea tridentata* was highly variable in burns which occurred from June through September. O'Leary and Minnich (1981) found moderate sprouting following the July 1973 burn. We observed nearly 100% sprouting following a small burn near Snow Creek in June 1983, but heavy mortality in another burn 2 weeks later 10 km NW. The 1980 burns (July, August-September) caused heavy mortality. These trends indicate that sprouting rates are more related to fire intensity than season of burning.

Heavy *Encelia farinosa* and *Ambrosia dumosa* mortality at Palm Springs parallels findings in Arizona (*A. deltoides*: Rogers and Steele, 1980) and California coastal sage scrub (Malanson and O'Leary, 1982). The reduction of *Opuntia acanthocarpa*, and *O. bigelovii* is comparable to that in burns at Snow Creek (O'Leary and Minnich, 1981), the Borrego Desert (Tratz and Vogl, 1977), and Arizona (Rogers and Steele, 1980). The vigorous sprouting of wash species (*Hyptis emoryi*, *Beloperone californica*, and *Acacia greggii*) at Palm Springs was also observed in similar habitats in the Borrego Desert (*Chilopsis linearis*, *A. greggii*, Tratz and Vogl, 1977). Such sprouting behavior may be a generalized adaptation to flash flood disturbances (Tratz, 1978; Zedler, 1981).

Poor seedling establishment at Palm Springs is probably unrelated to seed availability since all species occur in adjacent unburned areas. Most are capable of long-range seed dispersal by wind (*Larrea tridentata*, *Ambrosia dumosa* and *Encelia farinosa*) or fauna (*Opuntia bigelovii* [vegetative reproduction], *O. acanthocarpa*, *Hyptis emoryi* and *Beloperone californica*) (Ridley, 1930). Scattered resprouts and unburned individuals throughout the burns provide local seed sources. Thus, postfire habitats were apparently unfavorable for establishment.

Reproduction may be encouraged by disturbance. In powerline and road construction disturbances in the Mojave Desert, seedling establishment was most prolific among short-lived species, primarily *Encelia frutescens*, while germination of most long-lived species, including *Larrea tridentata* was limited (Vasek, 1980). We found no evidence of abundant *L. tridentata* reproduction, as reported in Arizona burn sites (Dalton, 1962). In an investigation following severe flooding near Ocotillo, Calif., Zedler (1981) recorded abundant reproduction of *Ambrosia dumosa*, *E. farinosa*, *Larrea tridentata*, *Opuntia echinocarpa*, *Acacia greggii*, *Hyptis emoryi* and *Beloperone californica*. Since postfire establishment was limited in the Palm Springs sites, prolonged surface moisture from abundant rainfall or floodwaters may be required for comparable germination and establishment.

Season of rainfall may have inhibited establishment of several shrubs. In Joshua Tree National Monument (50 km NE), Went (1948) found that *Acacia greggii*, *Dalea* spp., *Hymenoclea salsola*, *Hyptis emoryi* and *Larrea tridentata* germinated only in summer. Beatley (1974) suggested that summer rainfall is a requirement for successful germination of *L. tridentata*. However, unusually heavy summer rains at Palm Springs in August 1979 (44 mm), and the two wettest summers of the century (1983, 1984) resulted in only sporadic establishment of these shrubs. Similarly, Vasek (1980) found only limited germination of long-lived shrubs and succulents, including *L. tridentata*, *Opuntia acanthocarpa*, *Krameria grayi*, *Hilaria rigida*, in the Mojave Desert, despite favorable climatic conditions. *Encelia farinosa* responded prolifically to heavy winter rains of 1982-1983, a trend consistent with its distribution in coastal sage scrub of coastal southern California where summer rain is nearly absent. Zedler (1981) also observed heavy summer germination of this scrub.

Vasek (1980) suggested that soil condition, primarily the accumulation of organic matter, is important for germination. Many perennials at Palm Springs established seedlings only in burns. *Encelia farinosa* and *Ambrosia dumosa* establishment was also initially stimulated in burns. However, both shrubs colonized both burned and unburned sites after the wet 1982-1983 winter.

Desert succession studies elsewhere in California (Vasek *et al.*, 1975a, b; Vasek, 1980, 1983) indicate that most long-lived shrubs (*Larrea tridentata*, *Ambrosia dumosa*, *Opuntia bigelovii*, *Echinocereus engelmannii*, *Acacia greggii* and *Krameria parvifolia*) are characterized by limited but continuous establishment and thus respond negatively to disturbance. The chronic disturbance of desert habitats by wind and water erosion permits suitable sites for both short- and long-lived perennials. Creosote bush scrub stands are reported to occur in various successional states indicating continuous establishment. Postdisturbance regeneration may take hundreds of years to complete, being very slow at first (Vasek, 1980). The scale of such disturbances, however, is much smaller than wildland fires which can remove plant cover over extensive areas and exacerbate reestablishment by long-range seed dispersal.

The limited period of succession considered here permits only speculation on the future postfire succession at Palm Springs. Long-lived species were nearly eliminated and replaced by short-lived shrubs, mostly *Encelia farinosa*, with wash species persisting locally through sprouting. To date, there is little evidence of continuous long-lived perennial replacement as reported by Vasek *et al.* (1975b), in spite of favorable conditions provided by abnormally heavy precipitation. Indeed, 1984 aerial photographs (1:24,000; Riverside County Flood Control) indicate that *Larrea tridentata* has been removed from extensive areas of the San Jacinto Mountains. An open *Encelia farinosa* community now covering the slopes may persist for decades.

FIRE, CREOSOTE BUSH SCRUB STABILITY AND BIOGEOGRAPHY

In contrast with fire-prone chaparral and forest ecosystems covering the mountains of coastal California, many desert perennials appear unable to persist after burns by surviving fires, sprouting, fruit serotiny, long-term seed viability and immediate germination by scarification of soil seed (*see* reviews by Hanes, 1977; Wright, 1982; Reid and Oechel, 1984). Indeed, the rapid transformation of perennial cover and floristic composition of stands in the Palm Springs burns suggests that many creosote bush scrub taxa are poorly adapted to recurrent burning. Recurrent fire appears to select for short-lived desert shrubs, notably *Encelia farinosa* and *Ambrosia dumosa*, at the expense of long-lived species. At the Blaisdell site, the 1983 burn was carried entirely by herbs and eliminated the few shrubs which survived the 1980 burn. Field observations indicate that *Larrea tridentata* and *Opuntia echinocarpa* surviving a 1973 burn at Snow Creek were removed by the 1982 burn; the site is now covered by *Hymonoclea salsola* and annual grasses (*cf.*, O'Leary and Minnich, 1981).

The recent outbreak of fires, however, is clearly related to persistent above-normal precipitation and increases in native and exotic herb cover after 1976. It is important to ask whether recent burns are an aberration, and thus represent only an ephemeral event in creosote bush scrub ecology and biogeography.

Low mean annual precipitation and plant productivity at Palm Springs normally precludes short-term fire recurrences. Indeed, chaparral fires crossing the desert flanks of the San Jacinto Mountains earlier in the century stopped above desert scrub communities, owing apparently to limited fuel. Prehistoric burns doubtless extended into the desert margin on occasion when conditions were optimal. Disturbance intervals, however, were sufficiently long, perhaps centuries, to permit the establishment of long-lived desert perennials.

The western geographic limits of many taxa may thus be related to repeated, more intense burning associated with coastal sage scrub and chaparral. In southern California coastal sage scrub, burns are followed by rapid seedling establishment of *Eriogonum fasciculatum*, *Encelia farinosa*, *Salvia apiana*, *Salvia mellifera* and *Artemesia californica*, although resprouting is occasional (Malanson and O'Leary, 1982). Creosote bush scrub and coastal sage scrub are similar in that both ecosystems comprise mostly drought-deciduous mesophytic subshrubs. However, creosote bush scrub perennials, with the exception of *Salvia apiana* and *Encelia farinosa*, are poor colonizers following recurrent fire (Tratz, 1978). Indeed, recent burns have converted creosote bush scrub at Palm Springs to *Encelia farinosa* coastal sage scrub similar to stands covering semiarid interior valleys around Riverside, California.

Some desert taxa, including *Yucca schidigera*, *Simmondsia chinensis*, *Acacia greggii*, *Juniperus californica* and *Opuntia occidentalis*, extend westward into fire-prone areas of coastal southern California. These shrubs, however, are either vigorous sprouters (Tratz, 1978) or restricted to drier sites within the Pacific slope, such as at Aguanga and the Perris Plain in rain shadows of coastal ranges, and porous alluvial fans descending from the San Gabriel and San Bernardino mountains, where burning intervals are locally lengthened by low productivity (Axelrod, 1966; Smith, 1980).

The role of European exotics.—Recent burns, however, may have been encouraged by the profusion of European exotic grasses, especially *Bromus tectorum*, *B. rubens* and *Schismus barbatus*, during recent wet years. These species have continued to thrive during drier years since 1983. At Palm Springs, *B. rubens*, *Schismus barbatus* and other European grasses escape excessive summer heat through their winter annual habit. A minimum of cool-season precipitation (ca. 150 mm) appears sufficient to support these exotic grasses. In the dry interior, herbaceous cover resists decomposition resulting in accumulation of flammable fuels. Moreover, since exotic taxa may use desert habitats in ways distinct from indigenous taxa, consequent increases in herbaceous cover may thus increase fire frequencies and change the biogeography of creosote bush scrub without changes in climate.

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Competition Between Alien Annual Grasses and Native Annual Plants in the Mojave Desert

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ABSTRACT.—Alien annual grasses in the genera *Bromus* and *Schismus* are widespread and abundant in the Mojave Desert, and negative correlations between these aliens and native annual plants suggest that competition may occur between them. Effects of competition were evaluated by thinning alien annual grass seedlings and measuring the responses of native annual plants at three sites in the central, southcentral and southwestern Mojave Desert during 2 y of contrasting plant productivity. Effects of *Bromus* and *Schismus* were evaluated separately in the microhabitat where each was most abundant, beneath the north side of creosote bushes (*Larrea tridentata*) for *Bromus* and in the open interspace between shrubs for *Schismus*. Thinning of *Bromus* and *Schismus* significantly increased density and biomass of native annuals at all three sites, only during a year of high annual plant productivity and species richness. Effects of thinning were greatest for *Amsinckia tesselata* and for a group of relatively uncommon native annuals. Thinning also significantly increased the density and biomass of the alien forb, *Erodium cicutarium*. These results show that alien annual grasses can compete with native annual plants and an alien forb in the Mojave Desert and that effects can vary among years.

INTRODUCTION

Alien plants can alter the structure of native plant communities. In the Mojave Desert, biomass of alien annual plants is negatively correlated with biomass and species richness of native annuals, even when potential covarying factors such as disturbance and soil nutrient levels are accounted for (Brooks, 1998). In particular, biomass of alien annual grasses is negatively correlated with that of native annuals. These observations suggest that alien annuals may affect the community structure of natives in this region, possibly through interspecific competition.

Two of the most widespread and abundant alien annual plant taxa in the Mojave Desert are the annual grasses *Bromus madritensis* ssp. *rubens* (hereafter called *Bromus rubens*) and *Schismus* spp. (Brooks, 1998; Kemp and Brooks, 1998; Brooks and Berry 1999). These alien grasses affect native desert annuals by promoting wildfires (Brooks, 1999a) and possibly by competing with them for limiting resources such as nitrogen (Brooks, 1998) and water (Eissenstat and Caldwell, 1988; Melgoza and Nowak, 1991). *Bromus rubens* is invasive in its Mediterranean home range and is considered a wildland weed in the Mojave Desert (Brooks, 2000a). It has been present in this region since the early 1900s, but appears to have significantly increased in dominance since the 1970s (Hunter, 1991). *Schismus* spp. (*Schismus arabicus* and *Schismus barbatus*) is not invasive in its Middle Eastern home range, but is considered a wildland weed in the Mojave Desert (Brooks, 2000b). *Schismus* spp. invaded this region during the 1940s and apparently became dominant by the 1950s (O.

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Clarke, pers. comm.). Two other alien annual grasses, *Bromus tectorum* and *Bromus trinii*, are locally abundant but not as widespread and common as *Bromus rubens* and *Schismus* spp. (Brooks, 1998; Kemp and Brooks, 1998; Brooks and Berry 1999).

Although competition has been shown to occur among native desert annuals (Went, 1949; Klikoff, 1966; Inouye *et al.*, 1980; Kadmon and Shmida, 1990; Pantastico-Caldas and Venable, 1993; Venable *et al.*, 1993), it has rarely been demonstrated between native and alien species (Sonoran Desert: Inouye *et al.*, 1980; Pake, 1993; Mojave Desert: Hunter, 1995). Competition between *Bromus rubens* and native annual plants was evaluated in the northern Mojave Desert by experimentally reducing its dominance by thinning and by applying a grass specific herbicide (Hunter, 1995). Although these treatments increased the average density, biomass and species richness of native annual plants, the results were not statistically significant, possibly because of insufficient sample sizes. Competition between *Schismus* and native annuals was reported in the Sonoran Desert where fecundity of *Schismus barbatus* was compared with fecundity of the native annuals *Plantago patagonica* and *Pectocarya recurvata* (Pake, 1993). At high levels of annual plant productivity, fecundity of *Schismus barbatus* was significantly higher than that of the native species, but results varied among productivity levels suggesting that the competitive hierarchies were variable. The competitive effects that dominant alien plants have on natives and the conditions where competition is most likely to occur need to be understood to effectively conserve and restore native plant communities.

The purpose of this study was to test the hypothesis that alien annual grasses in the genera *Bromus* and *Schismus* compete with native annual plants in the Mojave Desert. Competitive effects can be caused by a variety of mechanisms, including interference competition, exploitation competition, apparent competition and higher order interactions (Goldberg and Scheiner, 1993). The common characteristic of these mechanisms is that absolute abundances of plants are higher when and where abundances of their competitors are reduced. The net effect of all possible types of competition is documented in this study.

Competitive effects of alien annual grasses on native annual plants were evaluated by comparing plots that were thinned of alien grasses to unthinned reference plots. Effects were evaluated among three sites and between 2 y to evaluate spatial and temporal variation in competition. The competitive effects of *Bromus* and *Schismus* were evaluated in separate experiments because effects of aliens often vary among taxa (Lodge, 1993).

METHODS

Study sites.—Three individual 1 ha study sites were established in the central, southcentral and southwestern Mojave Desert (Rowlands *et al.*, 1982). The site within each region was located at least 25 m from dirt roads, 1 km from paved roads, 2 km from human habitations, on undeveloped land managed by the United States Department of the Interior, Bureau of Land Management. All sites had granitic soils from the early to middle Holocene which are typical of these regions of the Mojave Desert. Soils at the southwestern site were well drained, gravely, Randsburg sandy loams less than 30 cm deep over a granitic pediment (Valverde and Hill, 1981). Soil surveys were not available for the other two sites, but soils were of similar granitic sandy loam. Longterm rainfall patterns at each site were estimated by averaging the distance-weighted, monthly precipitation averages from the three closest National Oceanic and Atmospheric Administration weather stations (U.S. National Oceanographic and Atmospheric Association, 1995). Winter rainfall amounts were recorded every two weeks from October through April during this study using a single rain gauge at the center of each site.

All sites contained creosote bush scrub plant communities (Munz, 1968) dominated by winter annual plants. Winter annuals germinate from September through December and remain as small vegetative tufts or rosettes until March or April when they rapidly grow, reproduce and die by May (Mulroy and Rundel, 1977). There are over 100 species of winter annuals compared to approximately 15 species of summer annuals in the Mojave Desert (Rowlands *et al.*, 1982). The dominant alien plants at all three sites were the winter annual grasses *Bromus rubens* and *Schismus* spp. and the forb *Erodium cicutarium*. The native winter annual grasses *Vulpia microstachys* and *Vulpia octoflora* were present at all sites, but were uncommon. Plant nomenclature followed Hickman (1993).

The central Mojave site was located south of Black and Opal mountains near Water Valley, San Bernardino County, California (35°07′30″N, 117°07′45″W) at 800 m elevation on a south facing alluvial bajada with 0–3% slope. Long-term average winter rainfall was 79 mm. The perennial plant community was dominated by *Larrea tridentata* and *Ambrosia dumosa*, but also included *Pleuraphis rigida* and *Achnatherum hymenoides*. No livestock grazing was permitted at this site since 1994 (U.S. Fish and Wildlife Service, 1994) and off highway vehicle (OHV) use was limited to roads and a few trails since 1980 (U.S. Bureau of Land Management, 1980a, b).

The southcentral Mojave site was located at the northern edge of the Ord Mountains, San Bernardino County, California (34°41′30″N, 117°57′30″W) at 1100 m elevation on a northwest facing alluvial bajada with 0–5% slope. Longterm average winter rainfall was 78 mm. *Larrea tridentata* and *Ambrosia dumosa* dominated the perennial plant community. No livestock grazing was permitted at this site since 1994 (U.S. Fish and Wildlife Service, 1994) and OHV use was limited to roads and a few trails since 1980 (U.S. Bureau of Land Management, 1980a, b).

The southwestern Mojave site was located at the southwest tip of the Rand Mountains in the Desert Tortoise Research Natural Area, Kern County, California (35°14′30″N, 117°51′15″W) at 870 m elevation on a southwest facing alluvial bajada with 0–5% slope. Longterm average winter rainfall was 104 mm. *Larrea tridentata* and *Ambrosia dumosa* dominated the perennial plant community. This site was closed to OHV use in 1973 and livestock grazing in 1976 (U.S. Bureau of Land Management, 1980ab). Further descriptions of the southwestern Mojave site can be found in Brooks (1999b).

Thinning treatments.—Effects of competition were tested by thinning the seedlings of two dominant alien annual grass genera, *Bromus* and *Schismus*, at the beginning of the growing season and evaluating the effects of thinning on density and biomass of native annuals at the end of the growing season. The relative composition of *Bromus* seedlings that were thinned was estimated because the individual species were difficult to distinguish as seedlings. *Bromus* seedlings were composed of approximately 90% *Bromus rubens* and 10% *Bromus tectorum* and *Bromus trinii*. The relative composition of *Schismus* seedlings that were thinned could not be reliably estimated.

Bromus and *Schismus* seedlings were thinned in the microhabitat where each was most abundant (Samson, 1986; Brooks, 1998; Brooks 1999c) and therefore most likely to compete with natives. *Bromus* seedlings were thinned beneath the canopy on the north side of creosote bushes (*Larrea tridentata*) (beneath-canopy microhabitat). *Schismus* seedlings were thinned in the open space between the canopies of perennial shrubs and bunchgrasses (interspace microhabitat). Seedlings were thinned using forceps and scissors and disposed of away from the plots. All aboveground portions of living plants were removed, leaving the roots intact and the soil undisturbed. Thus, alien annual grass seedlings were not completely removed, but their overall rates of photosynthesis and consumption of nutrients were reduced compared to unthinned reference plots.

Thinning treatments began when seedlings emerged approximately two weeks after the first and only cohort of annual plants germinated during each year. The time that the treatments began varied by two weeks among sites within each year. All treatments began in January, ended in February and consisted of an initial thinning followed by a second thinning two to three weeks later. In 1996, the average number (±1 SE) of *Bromus* seedlings thinned per 500 cm^2 plot was 128 ± 14 and the average number of *Schismus* thinned was 29 ± 4. In 1997, the average number of *Bromus* seedlings thinned per plot was 253 ± 33 and the average number of *Schismus* thinned was 52 ± 12.

Thinning experiments of this type are commonly used to evaluate competition in situ within plant communities, but they have problems (Campbell *et al.*, 1991; Goldberg and Barton, 1992). One problem is that soil disturbance and root death of thinned plants can affect soil microbial processes and the amounts of mineral nutrients such as nitrogen (Wilson and Tilman, 1991; McLennan *et al.*, 1995). Thus, effects of thinning can be erroneously attributed to competitive release when they are actually a result of altered levels of soil nutrients. Another problem is that thinning effects can vary within years depending on the phenological stages of plant species when thinning is applied (Campbell *et al.*, 1991), and possibly among years depending on the productivity and species composition of annual plant seedlings. These potential confounding effects were evaluated in the current study by monitoring levels of nitrate and ammonium in the soil of thinned and reference plots, thinning during years when only one cohort of seedlings emerged, and documenting community biomass and species composition during each year.

Experimental and sampling design.—Experimental factors were replicated at 25 stations arranged in a 5 × 5 grid at 25 m intervals within each of the three study sites. At each station four contiguous 20 × 25 cm (500 cm^2) experimental plots were placed end-to-end on their long axes in each of two microhabitats. For the *Bromus* thinning experiment, the experimental plots were placed in the beneath-canopy microhabitat of the closest creosote bush located in a random compass direction from each station. The four plots were oriented in an arc (~30°) corresponding to the position of the beneath-canopy microhabitat. Beneath-canopy microhabitats were only used for creosote bushes with canopy diameters of at least 150 cm so the four experimental plots would fit completely within this microhabitat. For the *Schismus* thinning experiments, the experimental plots were placed in the closest interspace microhabitat located in a random compass direction >1 m from the creosote bush used for the beneath-canopy microhabitat at each station. The four plots were placed end to end in an arc of the same shape as described above for the beneath-canopy microhabitat. Individual experimental plots were randomly assigned a single level of each experimental factor, treatment (thinning and reference) and year (1996 and 1997). Hence, two plots served as thinning and reference plots during 1996 and two others served as thinning and reference plots during 1997. The total number of treatment plots was 600 (2 years × 2 treatments × 2 species(microhabitats) × 25 stations × 3 sites).

The responses of native annual plants to the thinning treatments were evaluated by collecting annual plant samples when winter annuals reached peak biomass and before they began to senesce. Samples were collected 10–18 April 1996 and 9–17 March 1997. Live annual plants were clipped at ground level within 10 x 20 cm sampling frames, counted by species, dried to a constant mass at 60 C and weighed to determine aboveground live dry biomass. Each sampling frame was centered within the 500 cm^2 experimental plots. Samples from the 2 y were considered repeated measures, because they were collected within 1 m of each other from the same microhabitat located within each station at each site.

Soil samples were collected from a random subset of six sampling frames in each of the two microhabitats after annual plants were harvested in March 1997. Samples were 8 cm diameter by 7 cm deep and were centered within the sampling frame. Soils were immedi-

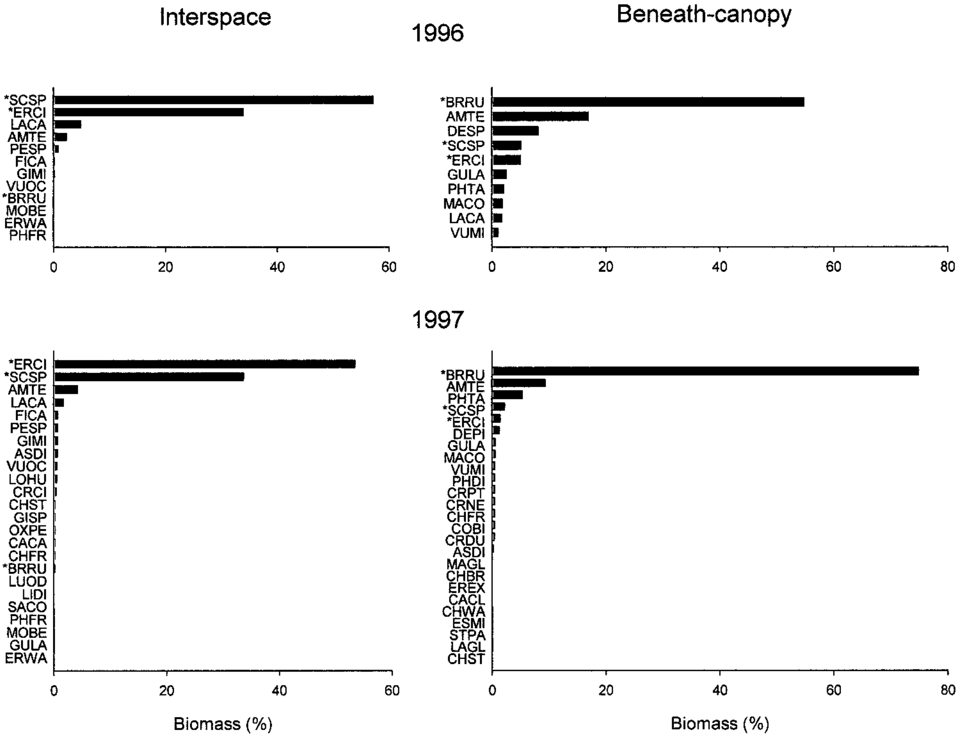

FIG. 1.—Percent biomass of annual plant species in interspace and beneath canopy microhabitats in 1996 and 1997. Species codes are defined in Appendix A; * = alien species

ately sieved (2 mm), stored in airtight plastic bags and analyzed by the University of California, Davis, Division of Agricultural and Natural Resources Analytical Laboratory.

Analysis of data.—Five dominant native annual plant taxa were evaluated individually, and the remaining less dominant native annuals were evaluated collectively as a group called "other natives" ($n = 6$ response variables). The dominant taxa had the highest density and biomass among natives within each microhabitat during both years at all sites, although their order of dominance varied between years (Fig. 1). The composition of the other natives group varied between microhabitats and between years. For the *Bromus* experiment, the response variables included *Amsinckia tesselata, Descurania pinnata, Malacothrix coulteri, Gullenia lasiophyllum, Phacelia tanacetifolia* and other natives. For the *Schismus* experiment, the response variables included *Amsinckia tesselata, Filago californica, Gilia minor, Lasthenia californica, Pectocarya* spp. and other natives.

Treatment effects were evaluated separately for *Bromus* thinning in the beneath-canopy microhabitat and *Schismus* thinning in the interspace microhabitat. All treatment-by-site, treatment-by-sampling station and treatment-by-site-by-sampling station interactions were not significant ($P > 0.250$), so these terms were pooled in the final model (3 sites × 25 sampling stations = 75 spatial replicates) (Underwood, 1997). The final general linear model was balanced with two fixed factors, treatment nested within year. Data were transformed using square root ($x + 0.5$) for density and species richness and $\log_{10}(x + 1)$ for biomass (Sokal and Rohlf, 1995). These transformations made the data more normally distributed and homoscedastic.

The data were analyzed in four steps. First, graphical plots were created displaying the average density and biomass of the dominant native and alien annual plant taxa in thinning and reference treatments during 1996 and 1997. Dominant alien plants were included to evaluate the effects of thinning on the alien grass taxa that were thinned, and to evaluate potential indirect effects of thinning on natives that may have been mediated through alien taxa that were not thinned (*e.g., Erodium cicutarium*). Second, repeated measures analysis of variance (ANOVA) was used to evaluate the significance of thinning treatments on total density and biomass of all native annual plants combined during each of the two years ($\alpha \leq 0.050$). Expected mean squares and significance tests were calculated using the GLM procedure and REPEATED statement of SAS statistical software (SAS Institute, 1985). Third, multivariate analysis of variance (MANOVA) was used to evaluate the significance of thinning treatments within each year on the density and biomass of five dominant, native, annual plant taxa plus the other natives group (6 response variables). MANOVA was used instead of multiple univariate ANOVAs because it does not require equal correlations among the response variables, it reduces the chance of type I errors that can occur with multiple univariate analyses, and it allows analyses of relationships among response variables (Scheiner, 1993; von Ende, 1993). Hotelling T^2 statistic was used to evaluate multivariate differences between thinning and reference plots (Morrison 1967). Degrees of freedom for the F-value of each MANOVA were p and $(N_1 + N_2 + p - 1)$, where $p = 6$ (response variables) and $N_1 = N_2 = 75$ (replicates). Standardized canonical coefficients and graphical plots were used to evalute the relative effect of thinning treatments on each response variable. Expected mean squares, significance tests, and standardized canonical coefficients were calculated using the GLM procedure and the MANOVA statement with the CANONICAL option (SAS, 1988). This procedure produced values of Wilks' λ, from which the Hotelling T^2 statistic was calculated using the formula: $T^2 = (n - 1)(1 - \lambda/\lambda)$ (Khattree and Naik 1995). Fourth, the significance of the six response variables used in each MANOVA were evaluated individually using ANOVA and bonferroni corrected type I error rates ($P \leq 0.05/6$ tests $= 0.0083$) (Sokal and Rohlf, 1995).

RESULTS

The amount and temporal distribution of winter (Oct.–Apr.) rainfall was similar at the three study sites, but differed between years during this study. In 1995–1996, winter rainfall averaged 94% of average (82 mm) and occurred in small increments throughout the winter. In 1996–1997 rainfall averaged 77% of average (67 mm), but occurred mostly in December when rainfall was 307% of average for that month (46 mm). This high December rainfall stimulated mass germination of annual plants which resulted in high biomass and species richness of annual plants during spring 1997. In the interspace microhabitat, amounts were higher in 1997 than 1996 for average (±1 SE) annual biomass (1.05 ± 0.11 vs. 0.32 ± 0.15 g/200 cm^2) and species richness (6.78 ± 0.32 vs. 1.77 ±0.10 species/200 cm^2). In the beneath-canopy microhabitat, amounts were also higher during 1997 than 1996 for average annual plant biomass (4.21 ± 0.40 vs. 0.12 ± 0.02 g/200 cm^2) and species richness (8.06 ± 0.35 vs. 1.79 ± 0.08 species/200 cm^2). Species composition also differed between years, with many more native species present in 1997 than 1996 (Fig. 1). Forty three species of annual plants were collected in this study (Appendix A), three of which were aliens which composed the majority of the total community biomass (Fig. 1).

Thinning treatments did not affect the amount of nitrate or ammonium present in the soil at the time annual plants were collected on 9–17 March 1997. In the beneath-canopy

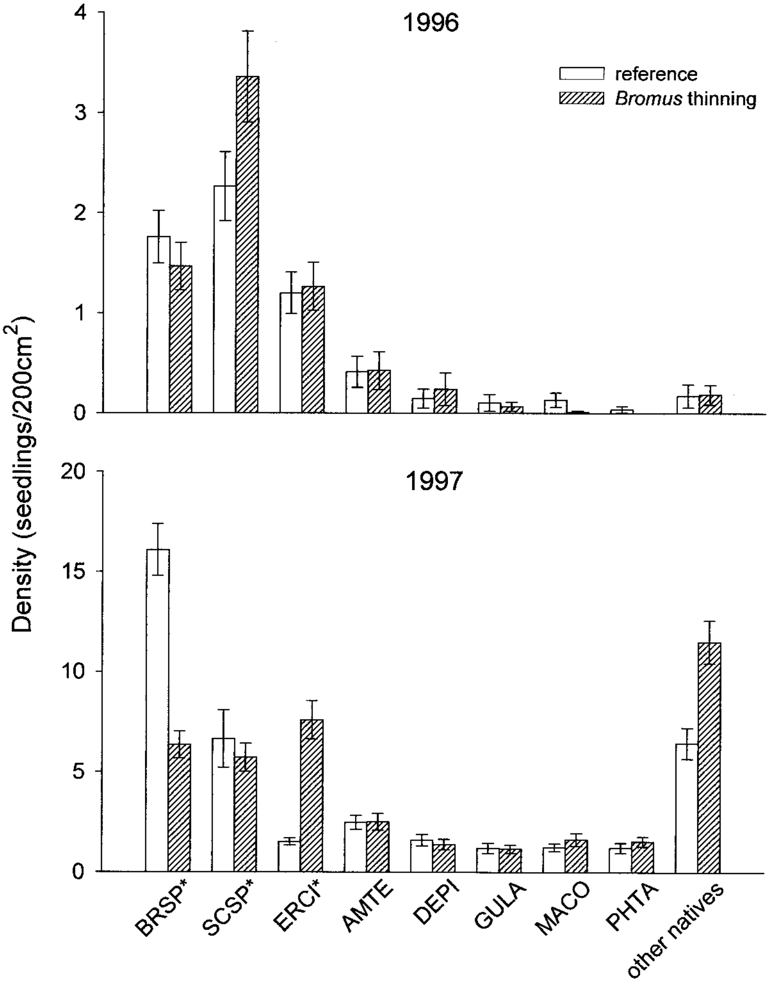

FIG. 2.—Effects of *Bromus* thinning on the density of annual plants in the beneath canopy microhabitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Descurania pinnata, Guillenia lasiophylla, Malacothrix coulteri, Phacelia tanacetifolia* and other native annuals. Species codes are defined in Appendix A; * = alien species

microhabitat, average (±1 SE) nitrate levels were 10.1 ± 1.1 ppm in treatment plots and 11.2 ± 0.9 ppm in reference plots, and ammonium levels were 3.4 ± 0.8 ppm in treatment plots and 3.7 ± 0.7 ppm in reference plots. In the interspace microhabitat, average nitrate levels were 4.8 ± 0.3 ppm in treatment plots and 4.9 ± 0.2 ppm in reference plots and ammonium levels were 1.1 ± 0.1 ppm in treatment plots and 1.0 ± 0.2 ppm in reference plots.

Effects of Bromus thinning.—Thinning reduced, but did not completely remove, density and biomass of *Bromus* in treatment compared to reference plots (Figs. 2, 3). In 1996 *Bromus* density was 17% and biomass was 4% lower in treatment than reference plots. In

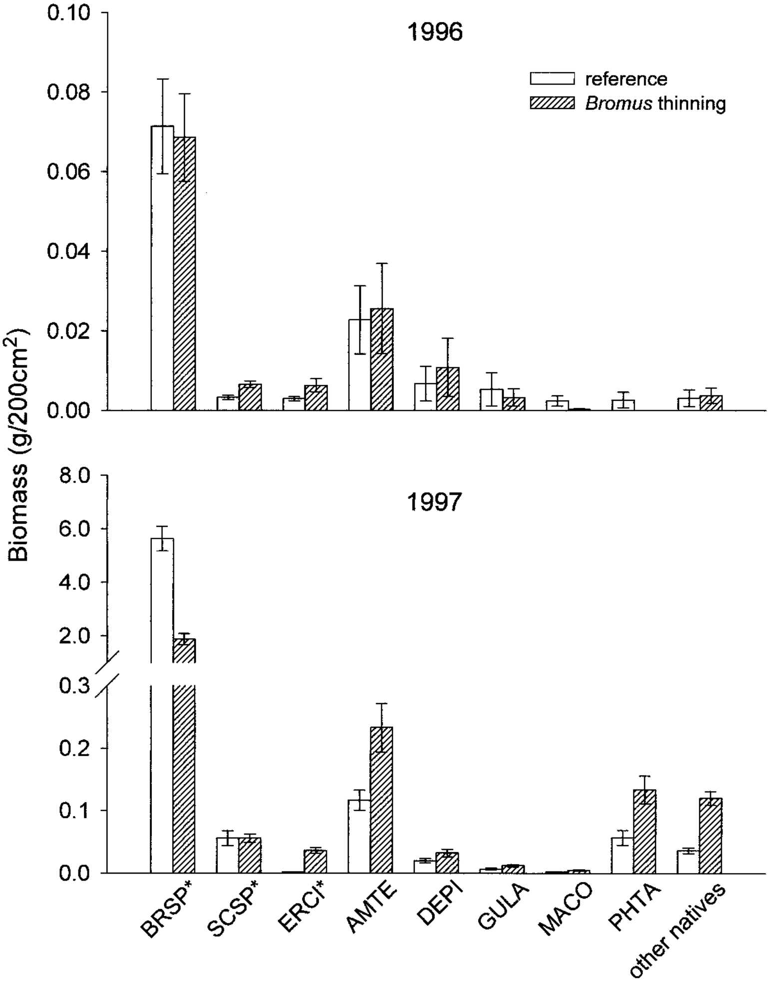

FIG. 3.—Effects of *Bromus* thinning on the biomass of annual plants in the beneath canopy microhabitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Descurania pinnata, Guillenia lasiophylla, Malacothrix coulteri, Phacelia tanacetifolia* and other native annuals. Species codes are defined in appendix A; * = alien species

1997, *Bromus* density was 61% and biomass was 67% lower in treatment than reference plots.

Thinning *Bromus* seedlings significantly affected the total density ($F_{1,148} = 8.53$, $P = 0.004$) and biomass ($F_{1,148} = 22.57$, $P < 0.001$) of native annual plants. Effects of thinning differed significantly between years, as indicated by significant treatment-by-year interactions for density ($F_{1,148} = 12.25$, $P = 0.001$), and biomass ($F_{1,148} = 35.15$, $P < 0.001$). Density and biomass of native annuals was significantly affected by thinning *Bromus* in 1997 ($F_{1,148} = 10.89$, $P = 0.001$ and $F_{1,148} = 32.58$, $P < 0.001$ respectively), but not in 1996 ($F_{1,148} = 0.03$, $P = 0.865$ and $F_{1,148} = 0.01$, $P = 0.980$ respectively). Density of natives (seedlings/

TABLE 1.—MANOVA of the effects of *Bromus* thinning in the beneath-canopy microhabitat on the density and biomass of *Amsinckia tesselata, Filago californica, Gilia minor, Lasthenia californica, Pectocarya* spp. and other native annuals

Response variable	Hotelling's T^2	F	df	P
1996				
Density	6.19	1.02	6, 143	0.412
Biomass	6.14	1.03	6, 143	0.407
1997				
Density	14.53	2.58	6, 143	0.021
Biomass	46.75	10.90	6, 143	<0.001

200 cm^2 ±1 SE) was 19.61 ± 1.43 on *Bromus*-thinned plots compared to 14.21 ± 0.88 on reference plots in 1997, and 0.93 ± 0.36 on thinned plots compared to 1.01 ± 0.29 on reference plots in 1996. Biomass of natives (g/200 cm^2) was 0.06 ± 0.02 on thinned plots compared to 0.05 ± 0.02 on reference plots in 1997, and 0.54 ± 0.06 on thinned plots compared to 0.24 ± 0.03 on references plots in 1996.

The multivariate effect of *Bromus* thinning on the six dominant native taxa was significant in 1997 but not 1996 (Table 1), although not all individual taxa were affected equally (Figs. 2, 3). For density, standardized canonical coefficients indicated that the other natives category was the group most affected by thinning treatments in 1997 (Table 2; $F_{1, 148} = 14.50$, $P < 0.001$). For biomass, other natives ($F_{1, 148} = 48.49$, $P < 0.001$) and *Amsinckia tesselata* ($F_{1, 148} = 7.63$, $P < 0.001$) were most affected by treatments.

Bromus thinning did not significantly reduce the density or biomass of *Schismus*, but did significantly reduce density and biomass of a third dominant alien, *Erodium cicutarium*, during 1997 (Figs. 2, 3). Density of *Erodium cicutarium* was significantly higher on thinned than reference plots in 1997 ($F_{1, 148} = 39.50$, $P < 0.001$) but not 1996 ($F_{1, 148} = 0.40$, $P = 0.884$), and biomass of *Erodium cicutarium* was significantly higher on thinned plots during 1997 ($F_{1, 148} = 57.11$, $P < 0.001$) but not 1996 ($F_{1, 148} = 3.76$, $P = 0.054$).

Effects of Schismus thinning.—Thinning reduced, but did not completely remove, density and biomass of *Schismus* in treatment compared to reference plots (Figs. 4, 5). In 1996, *Schismus* density was 81% and biomass was 65% lower in treatment than reference plots. In 1997, *Schismus* density was 90% and biomass was 83% lower in treatment than reference plots.

Thinning *Schismus* seedlings significantly affected the total density ($F_{1, 148} = 14.73$, $P < 0.001$) and biomass ($F_{1, 148} = 8.86$, $P = 0.003$) of native annual plants. Effects of thinning differed significantly between years, as indicated by significant treatment-by-year interactions

TABLE 2.—Standardized canonical coefficients of the first eigenvalue for the MANOVA of *Bromus* thinning in the beneath-canopy microhabitat on the density and biomass of native annual plant taxa during spring 1997. The magnitude of each coefficient corresponds to the relative effect of thinning on each response variable. Species codes are defined in appendix A

	AMTE	DEPI	GULA	MACO	PHTA	Other natives
Density	0.205	−0.202	−0.160	0.150	0.039	1.004
Biomass	0.462	0.072	0.217	0.263	0.173	0.850

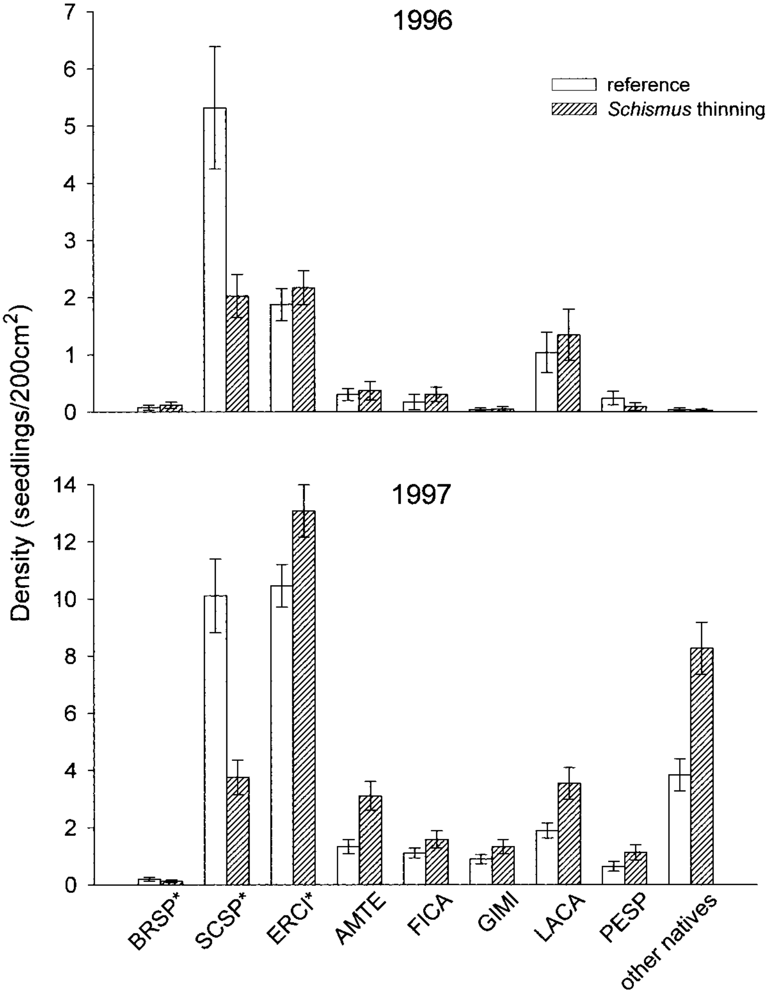

FIG. 4.—Effects of *Schismus* thinning on the density of annual plants in the beneath canopy microhabitat. Values represent the average of 25 replicates at three study sites ($n = 75$, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Amsinckia tesselata, Filago californica, Lasthenia californica, Pectocarya* spp. and other native annuals. Species codes are defined in Appendix A; * = alien species

for density ($F_{1,148} = 17.41$, $P < 0.001$), and biomass ($F_{1,148} = 15.42$, $P < 0.001$). Density and biomass of native annuals were significantly affected by thinning in 1997 ($F_{1,148} = 23.24$, $P < 0.001$ and $F_{1,148} = 14.05$, $P < 0.001$), but not in 1996 ($F_{1,148} = 0.07$, $P = 0.793$ and $F_{1,148} = 0.64$, $P = 0.426$). Density of natives (seedlings/200 cm^2) was 19.43 ± 1.40 on *Schismus*-thinned plots compared to 9.89 ± 0.75 on reference plots in 1997 and 2.12 ± 0.50 on thinned plots compared to 1.84 ± 0.40 on references plots in 1996. Biomass of natives (g/200 cm^2) was 0.18 ± 0.2 on thinned plots compared to 0.08 ± 0.01 on reference plots in 1997, and 0.03 ± 0.01 on thinned plots compared to 0.03 ± 0.01 on references plots in 1996.

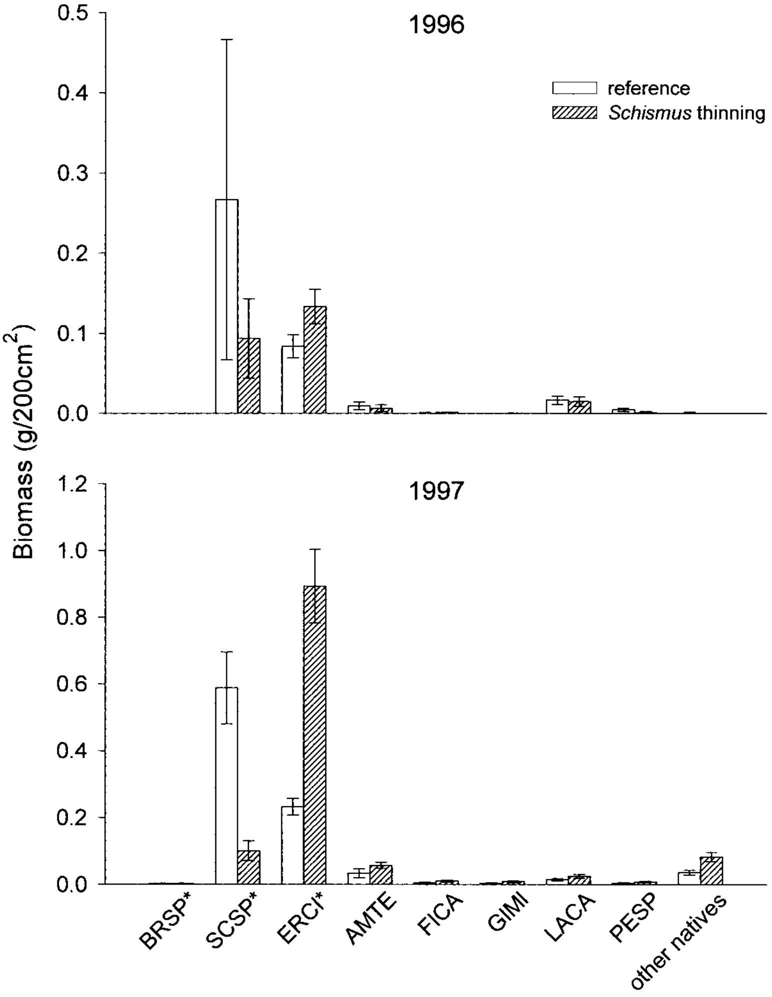

FIG. 5.—Effects of *Schismus* thinning on the biomass of annual plants in the beneath canopy microhabitat. Values represent the average of 25 replicates at three study sites (n = 75, +1 SE) for *Bromus rubens, Schismus* spp., *Erodium cicutarium, Amsinckia tesselata, Filago californica, Lasthenia californica, Pectocarya* spp. and other native annuals. Species codes are defined in Appendix A; * = alien species

The multivariate effect of *Schismus* thinning on dominant native taxa was also significant in 1997 but not 1996 (Table 3), although not all individual taxa were affected the same (Figs. 4, 5). Standardized canonical coefficients of density indicated that *Amsinckia tesselata* ($F_{1, 148}$ = 7.45, P = 0.007) and other natives ($F_{1, 148}$ = 12.63, P = 0.001) were the native taxa most affected by thinning treatments in 1997 (Table 4). Biomass of other natives was most affected by treatments in 1997 ($F_{1, 148}$ = 9.63, P = 0.002).

Schismus thinning did not significantly affect density or biomass of *Bromus* because *Bromus* was uncommon in the interspace microhabitat (Figs. 4, 5). After *Schismus* thinning, *Erodium cicutarium* significantly increased in density during 1997 ($F_{1, 148}$ = 4.98, P = 0.027)

TABLE 3.—MANOVA of the effects of *Schismus* thinning in the interspace microhabitat on the density and biomass of *Amsinckia tesselata, Descurania pinnata, Guillenia lasiophylla, Malacothrix coulteri, Phacelia tanacetifolia* and other native annuals

Response variable	Hotelling's T^2	F	df	P
1996				
Density	2.80	0.46	6, 143	0.840
Biomass	4.85	0.86	6, 143	0.570
1997				
Density	20.34	3.77	6, 143	<0.001
Biomass	14.50	2.57	6, 143	<0.001

but not 1996 ($F_{1,148} = 0.53$, $P = 0.469$), and in biomass during 1997 ($F_{1,148} = 39.99$, $P < 0.001$) but not 1996 ($F_{1,148} = 3.38$, $P = 0.068$).

Other observations.—Native annual plant seedlings in reference plots began to senesce approximately 2 wk earlier than those in thinned plots during 1997. Withering shoot tissue marked the onset of senescence. Many of these senescent seedlings died before they produced seeds and were not included in the samples of live annual plants collected in March 1997. The differential senescence of annual plants between treatments was not observed in 1996.

DISCUSSION

The results of this study support the hypothesis that competition occurs between alien annual grasses and native annual plants in the Mojave Desert. Thinning of alien annual grasses increased total density and biomass of native annual plants, but significantly affected only one of the five most dominant native species. This species, *Amsinckia tesselata*, is a common forb in disturbed areas of the Mojave Desert (Hickman, 1993). The results of this study should be interpreted cautiously because it was designed to evaluate the net effects of competition. Possible indirect effects between and among alien and native species prevent definitive conclusions regarding the mechanisms of competition. Evidence is discussed below that implicates certain mechanisms that are proposed as hypotheses for further study.

Thinning treatments can produce unwanted effects that complicate the interpretation of plant competition experiments (Campbell *et al.*, 1991; Goldberg and Barton, 1992), but these confounding effects were not detected in the current study. For example, thinning treatments did not affect levels of available nitrogen in the soil, indicating that thinning did not cause changes in soil fertility. In addition, the soil was left undisturbed on thinned plots, so surface disturbance was not a factor causing differences between treatment and

TABLE 4.—Standardized canonical coefficients of the first eigenvalue for the MANOVA of *Schismus* thinning in the interspace microhabitat on the density and biomass of native annual plants during spring 1997. The magnitude of each coefficient corresponds to the relative effect of thinning on each response variable. Species codes are defined in appendix A

	AMTE	FICA	GIMI	LACA	PESP	Other natives
Density	0.619	0.058	0.256	0.280	0.129	0.612
Biomass	0.470	0.312	0.239	0.140	0.061	0.633

reference plots. Alien annual grasses can also affect natives by altering fire regimes, biogeochemical cycles and rates of leaf litter accumulation (D'Antonio and Vitousek, 1992), but these effects should not occur within the four month interval of this experiment during each year. Thus, it seems reasonable to conclude that the effects of thinning were attributable to reduced net competition from alien annual grasses.

The mechanisms by which annual plants compete with each other result in different outcomes with respect to density and biomass. Densities of annual plants can either be affected by germination inhibition or by post-germination competition for limiting resources in the deserts of southwestern North America (Went, 1949; Juhren *et al.*, 1956; Inouye, 1980; Inouye *et al.*, 1980). In contrast, biomass of annual plants is affected primarily by post-germination competition (Inouye, 1991). In the current study there was only one cohort of annual plants that germinated each year and thinning treatments were applied after these seedlings germinated, so the effects of thinning should have been caused by post-germination competition.

Accelerated senescence of native annual plants in thinned compared to reference plots suggest that alien annual grasses competed with native seedlings for water and mineral nutrients as these nutrients became less abundant at the end of the growing season. *Bromus rubens, Schismus* spp. and *Erodium cicutarium* can assimilate nitrogen faster than native annuals in the central, southern and western Mojave Desert (Brooks, 1998), and *Bromus tectorum* can acquire water more rapidly than native annuals in the Great Basin desert (Eissenstat and Caldwell, 1988; Melgoza and Nowak, 1991). Nitrogen and water are considered to be the two primary factors that limit plant growth in the Mojave Desert (Rundel and Gibson, 1996). Hence, the competitive superiority of some alien annuals may be linked to competition for these nutrients. Experimental manipulations of seedling densities and nutrient levels are required to test this hypothesis.

Effects of thinning were similar at all three study sites and significant only during a year of overall high productivity, suggesting that competition of aliens with natives may be widespread but varies among years. However, these hypotheses require additional testing because site and year were fixed effects in this study. Moreover, the sites were all in plant communities dominated by the widespread and common perennial shrub *Larrea tridentata,* and interactions between alien and native annuals may be different in other plant communities. In addition, the 2 yr studied differed in biomass, species richness and species composition of annual plants, all factors that may affect competitive hierarchies. Studies documenting the net effects of competition should not be generalized beyond their spatial and temporal ranges, because the multiple mechanisms that influence these net effects can vary in space and time (Goldberg and Scheiner, 1993).

Thinning treatments increased the density and biomass of *Erodium cicutarium*, a widespread and abundant alien annual forb. This species has been present in southwestern North America since the 1600s (Mensing and Byrne, 1999), in contrast to most other exotic annuals that invaded during the late 1800s and early 1900s (Heady, 1988). The increase in density and biomass of *E. cicutarium* was approximately equal to the reduction of alien annual grass abundance on thinned plots, resulting in no net change in the proportional density and biomass of aliens (Brooks, 1998). Because the density and biomass of native annual plants increased despite similar increases in *E. cicutarium*, competition between them does not appear to have been significant. However, other evidence suggests *E. cicutarium* may compete with native annuals, based on negative correlations between their abundances in the Mojave (Brooks, 1998) and Sonoran Deserts (Inouye *et al.*, 1980). Tests of the relationships between *E. cicutarium* and native annuals are required to draw any reliable conclusions about their competitive relationships.

Bromus and *Schismus* may compete with different subsets of the native annual plant community, based on their respective dominance of the beneath-canopy and interspace microhabitats and because thinning of these taxa in the microhabitat where they were each uncommon did not affect native annual plants (Brooks, 1998). Because many native annuals display preferences for one or the other of these microhabitats (Shreve, 1931; Went, 1942; Muller, 1953; Halvorson and Patten,1975; Shmida and Whittaker, 1981), *Bromus* and *Schismus* may compete with different suites of annual plant species. However, there are areas in the Mojave Desert where *Bromus* density and biomass is high across the landscape in both microhabitats (Brooks, 1998), and in these areas *Bromus* may compete with a wider range of annual plants than was observed in the current study.

The composition of annual plant communities in the Mojave Desert can vary greatly among seasons and germination cohorts (Jennings, 1993; Burk, 1982), and the results of the current study may have differed given a different suite of annual plant seedlings. This study focused on winter-germinating annual plants that grew together in a single germination cohort during each of two years. It is unknown if the effects of thinning would have been different had a second cohort of annual plants germinated after the thinning treatments were applied each year. It is also unknown if these alien winter annuals compete with native summer annuals that grow from late winter through early summer. If alien winter annuals use large amounts of soil nutrients during winter and spring, then they may affect summer annuals by reducing the amounts of nutrients available during spring and summer. This hypothesis requires testing, especially in the eastern part of the Mojave Desert where summer annuals are most abundant (Rowlands *et al.*, 1982).

This study demonstrates that alien annual grasses can significantly affect the density and biomass of native annual plant seedlings. Years of competition from these grasses may reduce the seed banks of native annuals, possibly causing fundamental changes in annual plant community structure and food web dynamics. The results also highlight the need to evaluate the effects of all dominant alien taxa, because aliens such as *Erodium cicutarium* may increase in dominance when alien annual grasses are removed. This conclusion is especially important to keep in mind when implementing management practices designed to minimize the dominance of individual species of alien annual plants.

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SUBMITTED 5 APRIL 1998 ACCEPTED 17 JANUARY 2000

APPENDIX A.—Annual plants collected April 1996 and March 1997 at the DTNA

Amsinckia tesselata	AMTS	NF[1]	*Gilia minor*	GIMI	NF
Astragalus didymocarpus	ASDI	NF	*Gilia* species	GISP	NF
Bromus rubens	BRRU	AG	*Guillenia lasiophylla*	GULA	NF
Bromus species	BRSP	AG	*Lasthenia californica*	LACA	NF
Bromus tectorum	BRTE	AG	*Layia glandulosa*	LAGL	NF
Bromus trinii	BRTR	AG	*Linanthus dichotomus*	LIDI	NF
Camissonia campestris	CACA	NF	*Lotus humistratus*	LOHU	NF
Camissonia claviformis	CACL	NF	*Lupinus odoratus*	LUOD	NF
Chenactis fremontii	CHFR	NF	*Malacothrix coulteri*	MACO	NF
Chenactis steviodes	CHST	NF	*Malacothrix glabrata*	MAGL	NF
Chorizanthe brevicornu	CHBR	NF	*Monoptillon belliforme*	MOBE	NF
Chorizanthe watsonii	CHWA	NF	*Oxytheca perfoliata*	OXPE	NF
Coreopsis bigelovii	COBI	NF	*Pectocarya* species	PESP	NF
Crypthantha circumcissa	CRCI	NF	*Phacelia distans*	PHDI	NF
Crypthantha dumetorum	CRDU	NF	*Phacelia fremontii*	PHFR	NF
Crypthantha nevadensis	CRNE	NF	*Phacelia tanacetifolia*	PHTA	NF
Crypthantha pterocarya	CRPT	NF	*Salvia columbariae*	SACO	NF
Descurainia pinnata	DEPI	NF	*Schismus* species	SCSP	AG
Eremalche exilis	EREX	NF	*Schismus arabicus*	SCAR	AG
Eriophyllum wallacei	ERWA	NF	*Schismus barbatus*	SCBA	AG
Erodium cicutarium	ERCI	AF	*Stephanomeria parryi*	STPA	NF
Escholtzia minutiflora	ESMI	NF	*Vulpia microstachys*	VUMI	NG
Filago californica	FICA	NF	*Vulpia octoflora*	VUOC	NG

[1] AF = alien forb, AG = alien grass, NF = native forb, NG = native grass

DECLARATION OF SERVICE

I, Ileene Anderson, declare that on, May 21, 2010, I served and filed copies of the attached CBD Comments on RSPP Staff Assessment, dated May 21, 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: [http://www.energy.ca.gov/sitingcases/solar_millennium_ridgecrest].

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, in the following manner:

(Check all that Apply)

For service to all other parties:

_X_ sent electronically to all email addresses on the Proof of Service list;

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AND

For filing with the Energy Commission:

_X_ sending an original paper copy and one electronic copy, mailed and emailed respectively, to the address below (preferred method);

OR

____depositing in the mail an original and 12 paper copies, as follows:

CALIFORNIA ENERGY COMMISSION
Attn: Docket No. 09-AFC-9
1516 Ninth Street, MS-4
Sacramento, CA 95814-5512

docket@energy.state.ca.us

I declare under penalty of perjury that the foregoing is true and correct, that I am employed in the county where this mailing occurred, and that I am over the age of 18 years and not a party to the proceeding.

BEFORE THE ENERGY RESOURCES CONSERVATION AND DEVELOPMENT COMMISSION OF THE STATE OF CALIFORNIA
1516 NINTH STREET, SACRAMENTO, CA 95814
1-800-822-6228 – WWW.ENERGY.CA.GOV

APPLICATION FOR CERTIFICATION For the *RIDGECREST SOLAR POWER PROJECT*

Docket No. 09-AFC-9

PROOF OF SERVICE (Revised 4/30/2010)

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DECLARATION OF SERVICE

I, _______________, declare that on, __________________, I served and filed copies of the attached ____, dated __________. 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: [http://www.energy.ca.gov/sitingcases/solar_millennium_ridgecrest].

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AND

For filing with the Energy Commission:

__ sending an original paper copy and one electronic copy, mailed and emailed respectively, to the address below (preferred method);

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CALIFORNIA ENERGY COMMISSION
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