Does Protection of Desert Tortoise Habitat Generate Other Ecological Benefits in the Mojave Desert?

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Abstract—This paper summarizes the ecological effects of fenced habitat protection for the desert tortoise (*Gopherus agassizii*) at the Desert Tortoise Research Natural Area in the Mojave Desert. The following were higher inside than outside the natural area: (1) annual and perennial plant biomass, cover, diversity and dominance by natives, (2) soil seed biomass, (3) nocturnal rodent density and diversity, (4) breeding bird abundance and species richness, and (5) lizard abundance and species richness. The following were higher outside the natural area: (1) biomass of alien annual plants, and (2) abundance of black-tailed hares (*Lepus californicus*). Protection of habitat for the desert tortoise has resulted in higher abundance and diversity of many types of native plants and animals at this site.

Recovery plans for threatened or endangered species often require protection of very large areas from disturbances that threaten the species. Conservation biologists generally agree that these protected areas provide ecological benefits that extend far beyond the individual species for which they were created (Hudson 1991; Noss 1992). Benefits can range from the promotion of biodiversity to the maintenance of watershed functions. Although protection of habitat appears to be one of the most effective ways to preserve multiple levels of biological organization (Noss and Harris 1986; Falk 1991; Bloomgarden 1995), these effects are rarely documented and the general public remains largely unaware of them. This becomes a significant problem on public lands when the target species' population declines despite protection, and public land managers are pressured to reestablish multiple land-use activities.

Large areas of desert in southwestern North America are currently managed to protect the desert tortoise (*Gopherus agassizii*) and its habitat. In response to widespread population declines across its range, the desert tortoise was listed as a threatened species in 1990 in the Mojave and Colorado Deserts of California, Nevada, Arizona and Utah, west and north of the Colorado River (Fish and Wildlife Service 1990). The Desert Tortoise (Mojave Population) Recovery Plan proposed 14 Desert Wildlife Management Areas where local desert tortoise populations could be managed for recovery. (Fish and Wildlife Service 1994a). Criteria for the design of these management areas followed theory that was current during the early 1990s, and guidelines were established to determine their boundaries (Fish and Wildlife Service 1994a): (1) reserves should be distributed across the native range of the desert tortoise rather than confined to a small portion of the range; (2) large reserves are better than small reserves; (3) contiguous habitat is better than fragmented habitat; (4) habitat patches with less edge-to-area ratios are better than those with more; (5) closely spaced habitat patches are better than those spread far apart; (6) interconnected habitat patches are better than isolated patches; and (7) roadless habitat isolated from humans is better than habitat with roads and accessible to humans. These guidelines were used to establish areas of critical habitat for the desert tortoise in 1994, ranging from 221 to 4,130 km^2 each (Fish and Wildlife Service 1994b). This critical habitat (26,087 km^2), plus habitat already protected at Joshua Tree National Park (2,574 km^2) and at the Desert Tortoise Research Natural Area (DTNA) (100 km^2), total 28,761 km^2 of land protected for the desert tortoise (Berry 1997).

Critical habitat for the desert tortoise is managed to minimize the many threats to this species, most of which are related to human activities (Fish and Wildlife Service 1994a). These threats are summarized in a review of the Desert Tortoise (Mojave Population) Recovery Plan (Berry 1997). Despite habitat protection, densities of desert tortoises have continued to decline, primarily due to disease and predation of juveniles by ravens (Berry and others 1990a; Berry and others 1990b; Berry 1996). Protection of habitat may be insufficient to completely prevent the current decline in desert tortoise populations, but it is necessary for the ultimate recovery of the species.

Protection of desert tortoise habitat appears to also have other ecological benefits, and major bioregional ecosystem management plans have adopted the desert tortoise as an umbrella species for the conservation of many other taxa. This strategy assumes that habitat protection for an umbrella species will have multiple ecological benefits for sympatric populations, communities, or ecosystem components (Caro and O'Doherty 1999). Accordingly, the network of areas protected for the desert tortoise is assumed to have a wide range of other ecological benefits. Although the concept of the umbrella species is widely used, its effectiveness has not been empirically tested.

The DTNA, established in 1973, is the oldest area providing protection for the desert tortoise. Its boundaries were chosen to encompass a wide range of landforms, soils, elevations, and plant communities, all habitat factors that were considered important to the viability of the resident desert tortoises. The DTNA represents only a small fraction of the

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land protected for the desert tortoise, thus only a small fraction of the total effect of the desert tortoise as an umbrella species can be evaluated at this site. However, the DTNA provides an opportunity to test the hypothesis that abundance and diversity of native plants and animals are higher inside than outside of protected desert tortoise habitat. In this paper I use empirical data from published studies to evaluate the effects of habitat protection on a variety of plant and animal taxa at this site.

Site Description

The DTNA is located in the Fremont Valley and Rand Mountains of the western Mojave Desert, near California City, Kern County, California. The average annual rainfall for this region is 157 mm, 83% occurring between November and April. Mid-summer temperatures range from an average low of 19 °C to an average high of 34 °C, and mid-winter temperature averages in December range from 0 °C to 7 °C (National Oceanographic and Atmospheric Administration 1994). The woody plant community is dominated by creosote bush (*Larrea tridentata*) and burrobush (*Ambrosia dumosa*), with locally abundant patches of goldenhead (*Acamptopappus sphaerocephalus*), saltbush (*Atriplex polycarpa*), mormon tea (*Ephedra nevadensis*), goldenbush (*Ericameria cooperi*), California buckwheat (*Eriogonum fasciculatum*), cheesebush (*Hymenoclea salsola*), boxthorn (*Lycium andersonii*), Fremont dalea (*Psorothamnus fremontii*), cotton-thorn (*Tetradymia stenolepsis*), Joshua tree (*Yucca brevifolia*) and Mojave aster (*Xylorhiza tortifolia*) (Brooks 1995; Brooks 1999) Perennial grasses include Indian ricegrass (*Achnatherum hymenoides*) and desert needlegrass (*Achnatherum speciosum*), and small populations of bluegrass (*Poa secunda*). Cacti include small numbers of silver cholla (*Opuntia echinocarpa*) and beavertail cactus (*Opuntia basilaris*).

The western Mojave Desert was one of the first and most intensely used rangelands in the deserts of California (Bureau of Land Management 1980; Bureau of Land Management 1993). Extensive cattle grazing ceased in the 1930s, but sheep grazing continues to the present day. Recreational use of off-highway vehicles has been prevalent since the 1960s (Bureau of Land Management 1973). Since its creation in 1973, the DTNA has been closed to sheep grazing and vehicle travel has been limited to existing roads. Similar restrictions exist in other areas of critical habitat for the desert tortoise (Fish and Wildlife Service 1994a). Effective protection from trespass began in 1979-1980, when a 1 m tall fence of 15 x 15 cm “hogwire” hardware cloth was constructed along the perimeter. Trespass by sheep or off-road vehicles declined notably after this fence was constructed (Berry, personal communication). Sheep grazing and unrestricted off-highway vehicle use have continued in most areas adjacent to the DTNA, especially on private lands. The number of visitors to the DTNA increased steadily from 2,500 in 1982 to 8,000 in 1988 (Bureau of Land Management and California Department of Fish and Game 1988), but visitor use is largely confined to a small area near the interpretive center, more than 3 km from any of the study sites that I describe in this paper. Further descriptions of the disturbance history at the DTNA can be found in Brooks (1995; 1999).

Effects of Protection at the DTNA

This section summarizes a series of studies that measured differences in population and community variables of plants and animals inside and outside the DTNA. Study sites ranged from the northeast to the southwest parts of the DTNA and consisted of paired plots inside and outside the fenceline. Plots were matched for slope, aspect, elevation, soil type, and vegetation type and were located 400 to 1,000 m inside or outside the fenceline. The results are organized by taxa, and brief descriptions of methodologies are provided for each. Significance tests are identified in the tables, and statistical significance is reported at three levels, P - 0.10, 0.05, and 0.01. I sacrificed detail to maximize succinctness and clarity of the results. Detailed descriptions of these studies are contained in Brooks (1992; 1995; 1998; 1999).

Annual Plants

Aboveground live biomass and species richness of annual plants were measured at two sites during April 1990, 1991, and 1992 (Brooks 1992; Brooks 1995). When annual plants reached peak biomass and most species were flowering all annual plants within replicate 10 x 20 cm frames were cut at ground level, sorted by species, dried to a constant biomass at 60°C and weighed.

More species of annual plants had higher biomass (g/200 cm^2) inside than outside the DTNA during each year (table 1). Biomass of goldfields (*Lasthenia californica*) and comb-bur (*Pectocarya* spp.) were significantly higher inside in 1990, small-flowered poppy (*Eschscholzia minutiflora*) and goldfields were higher inside in 1991, and fiddleneck (*Amsinckia tessellata*), Mojave suncup (*Camissonia campestris*) and lacy phacelia (*Phacelia tanacetifolia*) were higher inside in 1992. The only species with higher biomass outside was the alien Mediterranean grass (*Schismus* spp.) during each of the three years. The biomass ratio of forbs to alien annual grasses was much higher inside than outside the DTNA (table 2), indicating that alien grasses were less dominant in the protected area. Species richness of annual plants was also higher inside than outside during each year, but differences were not statistically significant (table 1).

The difference in total annual plant biomass was very high inside versus outside the DTNA, but high inter-sample variance and conservative statistics limited levels of significance. For example, in 1990, aboveground live biomass (dry g/ha) was 12,325 inside and 4,740 outside (P = 0.22); in 1991, biomass was 199,460 inside and 57,770 outside (P = 0.17); and in 1992, biomass was 94,920 inside and 39,610 outside (P = 0.01).

Annual plants were sampled at five additional sites during 1994 and 1995 to determine the dominance of alien annual plants inside versus outside the DTNA (Brooks 1998). When annual plants reached peak biomass all annual plants within replicate 25 x 50 cm frames were cut at ground level, sorted by species, dried to a constant biomass at 60°C, and weighed. Biomasses and species richness of aliens were generally higher outside the DTNA, but results varied between years, and significance levels were weak (table 3).

Table 1—Annual plant biomass and species richness inside compared to outside the DTNA, April 1990-1992 (Brooks 1992, 1995).

	1990	1991	1992
Number of species with higher biomass inside[a]	5 of 6	17 of 18***	15 of 17***
Species with significantly higher biomass inside[b]	goldfields** (*Lasthenia californica*) comb-bur (*Pectocarya* spp.)	small-flowered poppy* (*Eschscholzia minutiflora*) goldfields**	fiddleneck*** (*Amsinckia tessellata*) Mojave suncups** (*Camissonia campestris*) lacy phacelia (*Phacelia tanacetifolia*)*
Species with significantly higher biomass outside	Mediterranean grass*‡ (*Schismus* spp.)	Mediterranean grass*‡	Mediterranean grass*‡
Species richness	higher inside	higher inside	higher inside

[a]Sign test
[b]Two-tailed paired *t* test
**P* - 0.10, ***P* - 0.05, ****P* - 0.01
‡Alien species

Perennial Shrubs

Density and cover of perennial shrubs were measured at two sites in June 1990 (Brooks 1992; 1995), and cover, height, volume and diversity were measured at two additional sites in June 1995 (Brooks 1999) using the point-quarter method (Greig-Smith 1964). Density of perennial shrubs was generally unaffected by protection, whereas cover and diversity were higher in the protected area (table 4). Estimates of cover were 33% (Brooks 1995) and 50% (Brooks 1999) higher inside than outside the DTNA. Cover of burrobush, California buckwheat, boxthorn and Fremont dalea were significantly higher in protected areas. Because cover was higher and density was generally unaffected by protection, the average size of individual shrubs was higher inside the DTNA. In an extreme case, Fremont dalea had higher density outside, but higher cover inside, indicating that individuals were much larger inside than outside the DTNA. Height diversity, cover diversity and volume diversity of perennial shrubs were all unaffected by protection (Brooks 1999). Species diversity was higher inside, but differences were either marginally significant (P - 0.10, table 4, Brooks 1995) or nonsignificant (Brooks 1999).

Soil Seed Biomass

Soil seedbank biomass was measured at two sites in April 1990, 1991 and 1992 (Brooks 1992; 1995). Samples were 6 cm diameter x 2 cm deep and consisted of both annual and perennial species. Biomass was higher inside than outside the DTNA during each year, but high inter-sample variance limited levels of significance (table 5).

Nocturnal Rodents

Nocturnal rodents were trapped at two sites on five occasions between March 1990 and February 1992 (6144 trap nights) (Brooks 1992; Brooks 1995). An 8 x 8 grid of Sherman live traps placed 10 m apart was used at each of the four paired plots. Animals were trapped four to six consecutive nights during the new moon to produce mark-recapture density and diversity estimates. Density of nocturnal rodents was higher inside than outside the DTNA, especially for the long-tailed pocket mouse (*Chaetodipus formosus*), Merriam's kangaroo rat (*Dipodomys merriami*) and southern grasshopper mouse (*Onychomys torridus*) (table 6). No species was more abundant in the unprotected areas. Species richness, evenness and the Shannon-Wiener diversity index were also significantly higher inside.

Table 2—Ratio of forbs to annual grasses inside and outside the DTNA, April 1990-1992 (Brooks 1992, 1995).

	1990	1991	1992
Inside the DTNA[a]	1,232**	34**	18**
Outside the DTNA	259	13	4**

[a]two-tailed paired *t* test of the difference between forb and grass biomass
***P* - 0.05

Table 3—Biomass and species richness of alien annual plants inside compared to outside the DTNA, April 1994 and 1995 (Brooks 1998). The area where each was highest is indicated for each year.

	1994[a]	1995
Red brome (*Bromus madritensis* ssp. *rubens*)	inside	outside**
Chilean chess (*Bromus trinii*)	outside	inside
Mediterranean grass (*Schismus* spp.)	outside*	outside
Filaree (*Erodium cicutarium*)	outside	inside
Total alien biomass	outside**	outside
Alien species richness	outside	outside

[a]Fisher's protected LSD test.
**P* - 0.10, ** *P* - 0.05

Table 4—Perennial shrub cover, density, and diversity inside compared to outside the DTNA, June 1990 (Brooks 1992, 1995).

	Cover	Density
Number of species higher inside[a]	11 of 13***	7 of 13
Total perennial shrubs[b]	higher inside	higher inside
Species significantly higher inside	burrobush** (*Ambrosia dumosa*) California buckwheat* (*Eriogonum fasciculatum*) boxthorn* (*Lycium andersonii*) Fremont dalea* (*Psorothamnus fremontii*)	none
Species significantly higher outside	none	Fremont dalea**
	Diversity	
Species richness	higher inside	
Evenness	higher inside*	
Shannon-Wiener index	higher inside*	

[a]Sign test
[b]Two-tailed paired *t* test
P* - 0.10, ** *P* - 0.05, * *P* - 0.01

Table 5—Soil seed bank biomass inside compared to outside the DTNA, April 1990-1992 (Brooks 1992, 1995).

	1990	1991	1992
Seed biomass[a]	higher inside	higher inside*	higher inside**

[a]Two-tailed paired *t* test
* *P* - 0.10, ** *P* - 0.05

Table 6—Nocturnal rodent densities and diversity inside compared to outside the DTNA, 1990-1992 (Brooks 1992, 1995).

	Density
Number of species higher inside[a]	4 of 5
Total nocturnal rodents[b]	higher inside*
Species significantly higher inside	long-tailed pocket mouse*** (*Chaetodipus formosus*) Merriam's kangaroo rat** (*Dipodomys merriami*) southern grasshopper mouse** (*Onychomys torridus*)
Species significantly higher outside	none
	Diversity
Species richness	higher inside***
Evenness	higher inside***
Shannon-Wiener index	higher inside***

[a]Sign test
[b]Two-tailed paired *t* test
P* - 0.10, ** *P* - 0.05, * *P* - 0.01

Table 7—Bird abundance and species richness inside compared to outside the DTNA during breeding and wintering seasons, 1994-1996 (Brooks 1999).

	Breeding season	Wintering season
Abundance[a]	higher inside***	higher inside
Species richness	higher inside***	higher inside
Species significantly higher inside	sage sparrow*** (*Amphispiza belli*) verdin** (*Auriparus flaviceps*) cactus wren* (*Campylorhynchus bunneicapillus)* ash-throated flycatcher** (*Myiarchus cinerascens*) LeConte's thrasher *** (*Toxostoma lecontei*) loggerhead shrike* (*Lanius ludovicianus*)	none
Species significantly higher outside	none	none

[a]Analysis of variance
P* - 0.10, ** *P* - 0.05, * *P* - 0.01

Table 8—Lizard abundance and species richness inside compared to outside the DTNA, 1994-1995 (Brooks 1999).

Abundance[a]	higher inside***
Species richness	higher inside*
Species significantly higher inside	western whiptail*** (*Cnemidophorous tigris*) desert spiny* (*Sceloporous magister*)
Species significantly higher outside	none

[a]analysis of variance
P* - 0.10, * *P* - 0.01

Table 9—Black-tailed hare (*Lepus californicus*) abundance inside compared to outside the DTNA, 1994-1995 (Brooks 1999).

Transect observations[a]	higher outside**
Fecal pellet counts[b]	higher outside***

[a]Analysis of variance
[b]Mann-Whitney U test
** *P* - 0.05, *** *P* - 0.01

Birds

Birds were censused at two sites on six occasions between May 1994 and January 1996 (Brooks 1999). A 4 x 4 grid of point-count stations placed 400 m apart was used at each of the four paired plots. Birds were censused for 2.5 h after sunrise during spring and winter seasons. Abundance and species richness of birds were higher inside than outside the DTNA, but differences were only significant during the spring breeding season (table 7). Sage sparrow (*Amphispiza belli*), verdin (*Auriparus flaviceps*), cactus wren (*Campylorhynchus bunneicapillus*), ash-throated flycatcher (*Myiarchus cinerascens*), loggerhead shrike (*Lanius ludovicianus*) and LeConte's thrasher (*Toxostoma lecontei*) were all significantly more abundant inside the DTNA during the breeding season. No species was more abundant in the unprotected areas.

Lizards

Lizards were censused at two sites on three occasions between July 1994 and July 1995 (Brooks 1999). Lizards were counted along six 1200 m parallel transects placed 400 m apart at each of the four paired plots. Censuses were conducted from 09:00 to 11:00 h PST. Abundance and species richness of lizards were higher inside than outside the DTNA (table 8). Western whiptail (*Cnemidophorous tigris*) and desert spiny (*Sceloporous magister*) lizards were significantly more abundant inside the DTNA, and no species was more abundant in the unprotected areas.

Black-Tailed Hares

Abundance of the black-tailed hare (*Lepus californicus*) was estimated using transect counts at two sites in May and July 1994 and using counts of fecal pellets at five other sites in April 1994 and 1995 (Brooks 1999). Individuals were counted along 1,200 m transects, and fecal pellets were counted within 25 x 50 cm sampling frames. Both methods indicated that black-tailed hares were significantly more abundant in the unprotected areas outside the DTNA (table 9).

Discussion

These data support the hypothesis that abundance and diversity of native plants and animals are higher inside than outside of protected desert tortoise habitat. Results from the DTNA may apply in other areas of protected desert tortoise habitat, for a number of reasons. Although the DTNA (100 km^2) is much smaller than other areas protected for the desert tortoise (typically >1,000 km^2), it is much larger than the home ranges of the wildlife studied. Most of the organisms found at the DTNA are also found throughout the geographic range of the desert tortoise. Disturbance effects at the DNTA are typical of those found adjacent to protected desert tortoise habitat elsewhere in its range. However, additional studies are required at other protected areas throughout its geographic range to comprehensively evaluate the desert tortoise as an umbrella species.

The one factor that may distinguish the DTNA from most other protected areas is the existence of a fence around its perimeter. Only Joshua Tree National Park has a similar fence. Trespass of sheep and off-highway vehicles was significantly reduced after the fence was constructed at the DTNA (Berry, personal communication). Unauthorized sheep grazing and off-highway vehicle use often occur adjacent to the DTNA, despite signs prohibiting these activities. It is likely that enforcement of land use restrictions is less effective where fences do not exist. Fenced areas need to be compared to unfenced areas with similar land use restrictions to determine the effectiveness of fencing as a management tool.

Protection from human disturbances can affect plants and animals directly or indirectly. Direct effects of human disturbance can include biomass removal, direct mortality or the alteration of behavioral patterns. Indirect effects may involve direct changes in an ecosystem component that secondarily affects others. For example, shrub cover was significantly lower outside than inside the DTNA, and this difference was likely due to the direct removal or damage to shrubs by sheep and off-highway vehicles. This effect on habitat structure may have secondarily caused the lower abundance and diversity of rodents, birds and lizards outside the DTNA. The one species with higher abundance outside, the black-tailed hare, prefers open habitats with minimal cover (Burt and Grossenheider 1976; Sosa Burgos 1991). Another potential indirect effect of protection is the prevention of plant biomass removal and reduced seed set and the secondary effects that the reduction in seed bank biomass has on granivorous wildlife (Brooks 1995). Protection may also prevent plant biomass removal and higher order effects on herbivorous arthropods and insectivorous vertebrates, although these relationships remain untested (Brooks 1999).

Current conditions inside and outside the DTNA are the result of approximately 20 years of limited protection (since establishment in 1973) and 10 years of effective protection (since fencing in 1980). Ecological differences between the protected and unprotected areas are likely due to both recovery from previous disturbance inside and further degradation from additional disturbance outside. In either case, protection of desert tortoise habitat has benefited a wide variety of plants and animals at this site.

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