

Environmental Characteristics of Desert Tortoise (*Gopherus agassizii*) Burrow Locations in an Altered Industrial Landscape

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ABSTRACT. – In the Colorado Desert of California, the western distributional limit of the desert tortoise (*Gopherus agassizii*) occurs in the Whitewater Hills of the southeastern San Bernardino Mountains. Much of the area has been developed for wind energy generation and tortoises often live in association with altered industrial landscapes. Natural habitat in the area was characterized by a sharp transition zone of plant associations including representatives of the Colorado and Mojave Deserts, coastal, and montane ecosystems. We examined the environmental factors associated with the locations of desert tortoise burrows at a site developed for wind energy generation. Measurements were taken at the opening of burrows, including elevation, slope, aspect, and distance to various natural and anthropogenic features of the landscape. We compared this data set with identical measurements for random points that lacked burrows in the same landscape. The analysis demonstrated that desert tortoises within the study area did not randomly select their burrow sites. Desert tortoise burrows were located closer to roads and concrete foundations associated with wind energy turbines and transformers than were random points. The results challenge the paradigm that desert tortoises are negatively affected by all forms of anthropogenic disturbance and suggest that with proper planning, some forms of development in the desert are compatible with conservation of sensitive species.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; burrows; wind energy generation; habitat selection; Mojave Desert; Colorado Desert; California; USA

Habitat use by animals is influenced by several factors that can have a dramatic influence on an individual's fitness. Selection of specific habitats can facilitate access to important resources such as food, water, mates and brood/nest sites, provide protection from predators and harsh environmental conditions, and limit competition with con- and hetero-specifics. When specific habitats are selected by animals, they are used disproportionately to their availability. Major assumptions of habitat selection are that animals select habitats that maximize their ecological requirements and fitness, and that high quality habitats are selected more than low quality habitats (Rosenzweig, 1981; Manly et al., 1993). In comparison with transient occupancy of habitat, location of nests, burrows, and other structures used by animals for longer periods of time represent a relatively long-term, and potentially costly, commitment to a particular microhabitat (Hansell, 1993). Consequently, the location of these structures has significant physiological and life-history consequences (Fig. 1).

The desert tortoise (*Gopherus agassizii*) is federally protected as a threatened species throughout about half of its range in the United States, which includes portions of California, Nevada, Arizona, and Utah (Fish and Wildlife Service, 1994). In California, as much as 98% of the annual activity cycle of the desert tortoise is spent underground in burrows or other shelter sites that it usually constructs (Nagy and Medica, 1986). Burrows are used for thermoregulation (McGinnis and Voigt, 1971; Zimmerman et al., 1994),

hibernation (Bailey et al., 1995; Rautenstrauch et al., 1998), nesting sites (Turner et al., 1986), and as foci for social interactions (Bulova, 1994, 1997). The location of burrows can also provide protection from flooding and fire. Burrows provide a special microhabitat where the humidity is higher and the temperature is lower and more constant than the environment on the surface. Thus, using burrows helps reduce evaporative water loss rates and provides protection from thermal extremes. Under adverse surface conditions, desert tortoises may stay in burrows for weeks or months at a time (Ernst et al., 1994).

Most research on the desert tortoise has focused on areas far removed from human population centers, although much of the habitat occupied by desert tortoises has been affected by humans to some extent (Lovich and Bainbridge, 1999), sometimes severely. Although human activities have been invoked as causes of population declines in the species (Fish and Wildlife Service, 1994; but see Corn, 1994, and Bury and Corn, 1995), few data are available to evaluate these impacts critically. The purpose of this study was to examine the environmental characteristics of desert tortoise burrow locations in an industrial landscape developed for wind energy generation near Palm Springs, California. Two questions were asked at the beginning of the study: (1) do desert tortoises randomly locate burrows in the study area? and, (2) if burrow locations are not random, do desert tortoises avoid constructing burrows in proximity to industrial activities?

METHODS AND MATERIALS

Site Description. — The study site was located on land administered by the Bureau of Land Management (BLM) in the Whitewater Hills of the southeastern San Bernardino Mountains in western Riverside County, California. The area, known locally as the Mesa wind park (Mesa), was developed for wind energy generation starting in the 1980s. Wind energy turbines and their associated infrastructure were the most conspicuous elements of the landscape with about 460 turbines, 51 electrical transformers, and an extensive network of unpaved roads in place at the time of the study (Fig. 2). Concrete foundations were associated with each turbine and electrical transformer. In addition, the area was grazed by cattle in most years as part of the Whitewater Grazing Allotment administered by the BLM. A vigorous breeding population of desert tortoises occupies the site (Lovich et al., 1999).

The study site was characterized by a mixture of plant communities representing several ecosystems. Sitting at the interface between coastally influenced plant associations and the desert, Mesa had exceptional perennial plant diversity. North-facing slopes and the western edge of the study area were dominated by chaparral and coastal sage scrub plant species (Schoenherr, 1992) including chamise (*Adenostoma fasciculatum*) and California sage brush (*Artemisia californica*). Other cismontane species (*sensu* Schoenherr, 1992) included California juniper (*Juniperus californica*), condalia (*Condalia parryi*), and isolated oaks (*Quercus* spp.). South-facing slopes and the eastern edge of the study area were characterized by typical Mojave Desert (Vasek and Barbour, 1977) and Colorado Desert (a subdivision of the Sonoran Desert, Burk, 1977) plants, including creosote bush (*Larrea tridentata*), burrobush (*Ambrosia dumosa*), honey mesquite (*Prosopis* spp.), cholla (*Opuntia* spp.), bladder pod (*Isomeris arborea*), linear-leaved



Figure 1. The location of a desert tortoise burrow can have dramatic consequences for its occupant. This photograph shows the carcass of a desert tortoise that died of third-degree burns in its burrow during a wildfire at the study site. The shallow burrow was located under a dense thicket of *Grayia spinosa* that ultimately became the funeral pyre for the animal. If the burrow would have been located in the open, or if it had been deeper, the occupant may have survived. Many of the tortoises at the site bear the scars of encounters with fire. Photo by JEL.

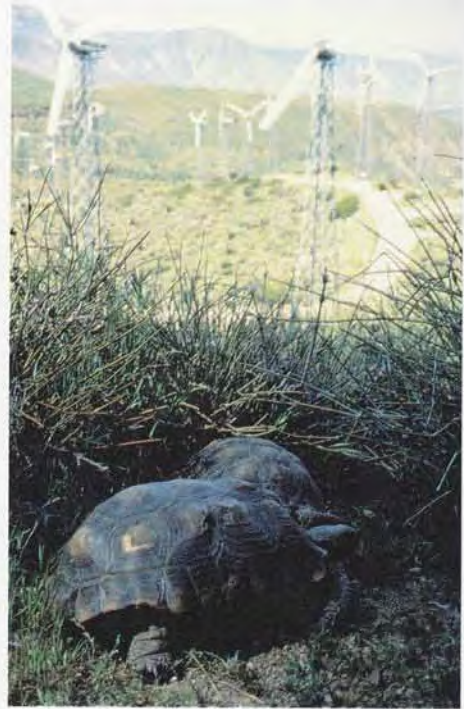


Figure 2. Partial view of study site showing wind energy turbines and desert tortoises (female in foreground, male in background) as they were found. The female bears the remnants of an old tag that was epoxied to her shell by a previous researcher for purposes of individual identification. Photo by JEL.

goldenbush (*Haplopappus linearifolius*), encelia (*Encelia farinosa*), and cheesebush (*Hymenoclea salsola*). A signature species of the Colorado Desert that occurred on site was teddy-bear cholla (*Opuntia bigelovii*). Another species, spiny hopsage (*Grayia spinosa*), a common plant of the Mojave Desert, but rare in the Colorado Desert except for the Whitewater Hills (Jaeger, 1940), was relatively abundant. The study site was mountainous with elevations at desert tortoise capture locations ranging from about 660 m in the valleys to over 880 m on the peaks and ridges. The topography at the northern boundary of the study site limited the distribution of tortoises, which usually occur below 1500 m (Germano et al., 1994), as elevation rises sharply to over 3500 m.

The study site was at the westernmost edge of the distribution of the desert tortoise in the Colorado Desert (Luckenbach, 1982; Patterson, 1982), where the steep terrain and unique plant associations are atypical of desert tortoise habitat elsewhere in the Colorado Desert (Fish and Wildlife Service, 1994). The coastally influenced climate resulted in greater rainfall than tortoise habitat immediately to the east, due to a rain-shadow effect, and this generally promoted high production of winter annual plants (Lovich et al., 1999) on which desert tortoises feed.

Methodology. — We collected data during 1995 and 1996, although anecdotal observations continued through 1998 during the course of our separate research on the reproductive ecology of desert tortoises at the site (Lovich et al., 1999). Burrows were located during systematic searches

Table 1. Desert tortoise (*Gopherus agassizii*) burrow attributes reported in the literature. Aspect refers to the predominant orientation of the entrance of the burrows.

Aspect	Slope	Cover Association	Region	Reference
North-northeast	—	72% under shrubs	southern Nevada	Burge, 1978
West-southeast	—	79% under shrubs	California deserts	Berry and Turner, 1986
North	—	—	southern Nevada	Bulova, 1994
South	44.1°	40% under shrubs	Arizona	Bailey et al., 1995
—	—	68% under perennial plants	California	Duda, 1998
Southwest	17.7°	41% under shrubs	Mesa, California	This study

of the wind park conducted by walking transects through areas bounded by unpaved roads or rows of turbines. Only burrows that were approximately shell-depth or more (thus excluding shallow excavations or pallets according to the definition of Burge, 1978), and known or appearing to be actively used, were included in the statistical analyses. All burrows but one, occupied by a juvenile, were typical of the size used by adult tortoises (18–37 cm carapace length, Ernst et al., 1994). The following variables were quantified for each burrow: SLOPE (in degrees), ASPECT (compass direction in degrees of the predominant facing slope), and ELEVATION. In addition, distances were measured from the opening of each burrow to various natural and anthropogenic features in the landscape, including the following variables: ROAD (unpaved roads, as no paved roads are located at the site), PAD (concrete foundations for turbines and electrical transformers), LARREA (creosote bush, *Larrea tridentata*), ENCELIA (brittlebush, *Encelia farinosa*), CACTUS (several cactus species of the genus *Opuntia*), YUCCA (*Yucca* spp.), and ROCK (rock outcrops or rockpiles). These variables were selected because they were prominent features of the landscape. Distance variables were measured using a flexible tape. All plants were alive at the time the burrow was constructed, although many were dead at the time of measurement due to the effects of a major fire in 1995. The importance of using fine scale habitat characteristics to infer ecologically meaningful patterns in desert tortoise burrow distribution has previously been demonstrated by Baxter (1988). Computer-generated random points were used to locate sites that did not have burrows and the same variables were measured. The statistical analysis included 32 desert tortoise burrows and 32 random points.

Following Zar (1984), data were transformed for statistical analyses using the natural logarithm of (x+1), unless indicated otherwise, to meet the assumption of normality. Multivariate Analysis of Variance (MANOVA) was used to assess the overall significance of differences between all

variables measured (except ASPECT) for burrows and random plots. This technique is superior to using multiple univariate ANOVAs because it uses correlations among characters rather than ignoring them (Willig et al., 1986). Principal components analysis (PCA) was then used on transformed variables, normalized to have a mean of zero and a standard deviation of one, as a data reduction technique to identify orthogonal factors and the variables that loaded highly in each. Separate MANOVAs were calculated for variables that loaded highly in each factor. Following identification of multivariate significance, a two-group discriminant function analysis (DFA) was conducted using the influential variables selected with PCA. The classification accuracy of the function was assessed by tabulating actual locations (burrows and random points) vs. locations predicted by the function.

Because ASPECT is a circular scale variable, it was analyzed separately using Oriana[®] software for circular statistics. Other statistical procedures were executed using SYSTAT (Wilkinson et al., 1992). Levels of statistical significance were set at an alpha of 0.05.

RESULTS

Of the 32 burrows analyzed, 13 (41%) were located under shrubs, including *Larrea*, *Ambrosia*, *Ephedra* sp., *Hymenoclea*, and *Grayia* (Table 1). One of the burrows included in our statistical analysis was located under the concrete pad of an electrical transformer (Fig. 3a). Subsequent observations made after our study concluded, but not included in our statistical analysis, demonstrated that this was not an unusual burrow location and that burrows were commonly associated with anthropogenic features in the landscape (Figs. 3b-f).

There were few significant differences among the variables measured, with YUCCA being the single exception (Table 2). However, the results of a MANOVA using log-

Table 2. Means, standard deviations (in parentheses), and ranges for variables measured at desert tortoise burrows and random points. The probability for ASPECT is based on Watson's F-test for two circular means. Probabilities for other variables are based on univariate F-tests (ANOVA) comparing the means of log-transformed data for burrows and random points. All measurements are in meters, except for slope and aspect, which are in degrees.

	SLOPE	ASPECT	ROAD	PAD	LARREA	ENCELIA	CACTUS	YUCCA	ROCK	ELEVATION
Burrows	17.7 (10.2)	188.3 (66.5)	22.1 (22.6)	49.7 (77.1)	16.8 (25.4)	5.1 (6.0)	4.8 (4.6)	31.7 (30.1)	10.3 (16.0)	770.3 (32.3)
Random	15.9 (10.7)	193.1 (97.3)	33.9 (41.5)	66.2 (59.2)	23.7 (45.4)	6.5 (5.9)	7.8 (9.7)	16.1 (18.4)	14.7 (14.1)	775.1 (29.0)
Probability	0.62	0.84	0.96	0.14	0.61	0.21	0.12	0.04	0.18	0.53



Figure 3. Desert tortoise burrows at the study site were frequently associated with human disturbances in the environment. All photos by JEL unless noted otherwise. **(a)** This female, visible in the center of the photograph, constructed her burrow under the concrete pad of an electrical transformer and shared it with a packrat (*Neotoma* spp.). Her frequent use of the burrow (spanning about 2 years) was shown by scratches on her carapace caused by passing under the concrete lip of the foundation. Photo by Claude Kirby. **(b)** Another female used a burrow under a different electrical transformer pad. The entrance is the wide area shown on the right side of the pad. **(c)** Yet another female constructed her burrow in the road cut next to a turbine. She deposited a clutch of eggs in the apron of her burrow in 1997. **(d)** Close-up of a juvenile desert tortoise (6.9 cm carapace length) at the entrance to the burrow shown in Fig. 3e. **(e)** A juvenile desert tortoise constructed a burrow under a piece of waste concrete next to a turbine. A lens cap (lower center of the photograph) is shown above the entrance to the burrow. **(f)** Desert tortoise burrows at the study site are frequently constructed in cut banks along roads. Note the burrow under the white marker pole.

transformed data for all variables except ASPECT, revealed significant differences among the variables characterizing burrows and random points (Wilk's Lambda = 0.730; $df = 9, 54$; $p = 0.035$). The mean vector for burrow ASPECT was southerly (188.3°) but it was not significantly different from the mean vector (193.1°) for random points (Watson's F-test, $F = 0.04$, $p = 0.84$, $df = 62$; Table 2, Fig. 4).

PCA revealed four principal components with eigenvalues greater than unity that together explained 74.7% of the total variance. The first principal component was related to anthropogenic features in the landscape as shown by high loadings for ROAD and PAD. The other principal components were related to distance to various plant species (Table 3). A simplified MANOVA using the highest loading vari-

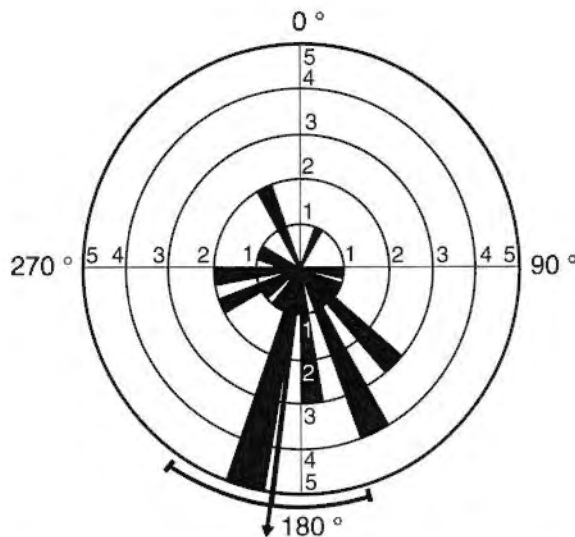


Figure 4. Plot of vectors showing aspect of slopes for locations with desert tortoise burrows. Bar width is 10°. Frequency is shown by the radius of wedge. The mean vector (188.3°) and the 95% confidence interval are shown.

ables in each principal component (PAD, LARREA, YUCCA, ENCELIA) was not significant (Wilk's Lambda = 0.870; $df = 4, 59$; $p = 0.080$). Because the first principal component was related to anthropogenic features, it seemed logical to include ROAD as another variable in MANOVA. Although ROAD and PAD were correlated as shown by their high loadings and same sign (Table 3), there were many occasions when the nearest road to a burrow or random point was not the road next to the nearest pad (which always had service road access). MANOVA using an expanded model including ROAD, PAD, LARREA, YUCCA, and ENCELIA approached significance (Wilk's Lambda = 0.839; $df = 5, 58$; $p = 0.064$).

The DFA on PAD, LARREA, YUCCA, and ENCELIA achieved an overall classification accuracy of 67.2% with most misclassifications occurring for burrows (Table 4). An expanded model including ROAD did not change the results appreciably, but a full model incorporating all variables, with the exception of ASPECT, achieved 71.9% classification accuracy (Table 5). The discriminant scores for burrows were significantly different than those for random points as shown by a two-tailed Student's t -test ($t = -4.788$, $df = 62$, p

Table 3. Unrotated principal component loadings for principal components with eigenvalues greater than one. Variance explained by each component is shown in parentheses.

Variable	Principal Component			
	I (30.717)	II (18.619)	III (13.354)	IV (12.106)
PAD	0.844	0.058	-0.280	0.011
ROAD	0.799	-0.336	-0.116	-0.008
ELEVATION	-0.724	-0.505	0.011	0.087
SLOPE	0.565	-0.449	0.443	0.108
LARREA	-0.476	-0.610	-0.043	0.452
CACTUS	-0.281	0.592	0.146	0.521
YUCCA	0.304	0.262	0.785	0.282
ENCELIA	0.244	0.272	-0.523	0.611
ROCK	-0.334	0.487	0.013	-0.377

< 0.001). A summary of habitat relationships based on discriminant scores is depicted in Fig. 5.

DISCUSSION

The results of our analysis demonstrate that desert tortoise burrow sites were not randomly located as shown by the results of MANOVA of log-transformed variables. This was not unexpected in that other investigators have demonstrated the preference of desert tortoises for certain environmental attributes. Baxter (1988) studied desert tortoise burrow locations near Twentynine Palms, California, approximately 50 km from our study site. He found that at the landscape level, burrow distribution was not statistically different from random. However, the abundance of burrows differed across six plant assemblages reflecting both the non-randomness of the plant assemblages in the landscape, and the preference of desert tortoises for certain assemblages, particularly along ecotones. At the same site (near Twentynine Palms), Duda (1998) found that tortoise burrow locations were statistically different from both random and Poisson distributions, with the data further suggesting that the underlying distributions were clumped.

Hibernation burrows of desert tortoises in the Sonoran Desert of Arizona are often associated with vegetation (dead or alive) and packrat (*Neotoma albigula*) nests (Bailey et al., 1995). Most hibernation burrows examined were located on steep (>45°) south-facing slopes in soils composed of silt, silt with loose gravel, diatomite and/or diatomaceous marl, or layers of well-lithified volcanic ash.

The characteristics of desert tortoise burrow sites in southern Nevada were studied by Burge (1978). Most burrows faced east, northeast, or north, and 72% were located under shrubs. Shrubs were utilized disproportionately to their abundance. For example, 37.7% of the burrows located under shrubs were found under *Acacia greggii* despite the low density of that shrub at the study site. According to Burge, the shade provided by *A. greggii* may have been the reason for its disproportionate use. Similarly, burrows were

Table 4. Classification accuracy of discriminant function analysis for variables PAD, LARREA, ENCELIA, and YUCCA. Row totals are in parentheses.

Actual Group	Predicted Group		Total
	Burrows	Random Points	
Burrows	20 (62.5%)	12 (37.5%)	32
Random points	9 (28.1%)	23 (71.9%)	32
Total	29	35	64

Table 5. Classification accuracy of discriminant function analysis for variables ROAD, PAD, LARREA, ENCELIA, YUCCA, SLOPE, CACTUS, ROCK, and ELEV. Row totals are in parentheses.

Actual Group	Predicted Group		Total
	Burrows	Random Points	
Burrows	22 (68.8%)	10 (31.2%)	32
Random points	8 (25.0%)	24 (75.0%)	32
Total	30	34	64

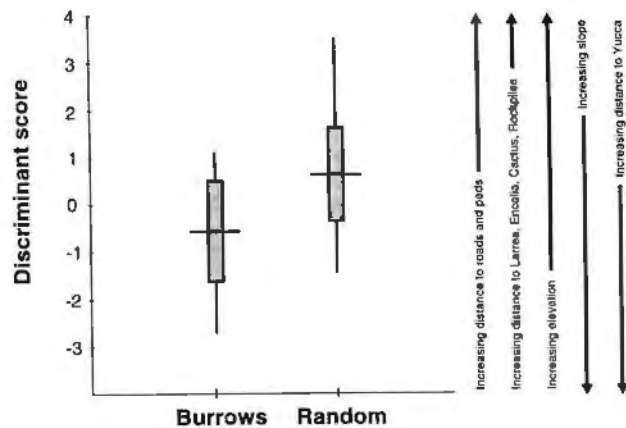


Figure 5. Plot of discriminant score statistics based on a full model incorporating log-transformed ROAD, PAD, LARREA, ENCELIA, YUCCA, SLOPE, CACTUS, ROCK, and ELEV. Means are shown with one standard deviation and ranges for burrows and random points. Arrows show direction of correlation among variables and discriminant scores. The means are significantly different at $p < 0.001$.

frequently located under *Yucca schidigera*, although this plant was numerically under-represented at the study site. Burge suggested that *Yucca* provided roof structure and possibly insulation for burrows. In sharp contrast, the results for our study showed that tortoise burrows were located farther from *Yucca* than were random points, a phenomenon for which we have no explanation.

More recently, Wilson et al. (1999) quantified the physical and microhabitat characteristics of burrows used by juvenile desert tortoises in a field enclosure located in the western Mojave Desert of California. The majority of burrows were located well under large shrub canopies, especially the two species *Larrea tridentata* and *Lycium pallidum*, than were located under the canopy margin or in the open. The mean angle of burrow orientation was 71°. The authors hypothesized that placement of burrows well under large shrubs conferred better protection from predators and/or provided more favorable microclimates for juvenile desert tortoises than burrows located under smaller shrubs or in the open.

Our analysis shows that the principal component explaining the greatest variance in burrow site attributes at Mesa was related to the proximity of anthropogenic features in the landscape. The question that needs to be addressed is: what factors encouraged adult desert tortoises at our study site to locate their burrows in close proximity to roads and turbines? This question is especially pertinent in recognition of well-established evidence showing that roads have generally negative consequences for wildlife due to: (1) mortality of animals along roadways (Rosen and Lowe, 1994; Boarman and Sazaki, 1996), (2) habitat fragmentation and restriction of movements and gene flow, and (3) increased access to remote areas for illegal collection and vandalism of plants and animals (Boarman and Sazaki, 1996). However, none of the roads at our study site are paved and the combination of light traffic (public access is strongly restricted) and generally slow vehicle speeds minimize direct mortality.

Desert tortoises may construct burrows along the elevated berms of unpaved roads because the topography mimics that formed along the banks of desert washes, a preferred site for burrow construction (Luckenbach, 1982). Of the 207 burrows observed by Burge (1978) in large washes, 151 were located in banks with the remainder in the channel bed. She also noted that the elevated dirt berms along roads served as burrow sites for a small portion of her sample. Because desert tortoises appear to prefer the steeply eroded banks of washes for burrow sites in some areas, they may not discriminate between natural banks and the elevated berms associated with most unpaved roads in the desert.

Another explanation for why tortoise burrows at Mesa tend to be located closer to roads than are random points stems from the fact that plant productivity in the desert is often greater along roadsides. "Edge-enhancement" of perennial shrubs along the margin of roads is substantiated by past research in the Mojave Desert showing that plants along roadsides are denser, larger, more vigorous, and support greater numbers of foliage arthropods than those away from roadsides (Vasek et al., 1975; Lightfoot and Whitford, 1991). Primary productivity, as measured by standing crop, increased about 17 times on the basis of vegetated area alone, and 6 times when the area of the bare, paved road surface was included as part of the calculated area. Unpaved roads showed increases of 6 and 3 times, respectively, in each category (Johnson et al., 1975). The increase in vigor has been shown to attract herbivorous insects (Lightfoot and Whitford, 1991), so it is conceivable that the herbivorous desert tortoise selects burrows in close proximity to high densities of food plants as well. In Florida, gopher tortoise (*Gopherus polyphemus*) densities are positively correlated with the percent herbaceous cover, an indicator of food resources (Breining et al., 1994).

Baxter (1988) found that high density plant ecotones were important determinants of desert tortoise abundance near Twentynine Palms, California, an area that is relatively close to our study site. The distribution of burrows observed by Baxter led him to conclude that desert tortoises are "edge" species. Again, desert tortoises may not discriminate between natural edges and those formed by roads. Similarly, Garner and Landers (1981) observed that roadsides and the edges of fields were common burrowing sites for *G. polyphemus* in Georgia. They also noted that vegetation in those areas generally contained more minerals than food plants on natural sand ridges.

Terrestrial desert chelonians sometimes include roads in their movement patterns. Nieuwolt (1996) observed that some individuals of *Terrapene ornata luteola* used roads to make most of their movements and that distances moved on roads were significantly greater than distances moved off-road. No explanation was offered for the observed difference but it seems logical that roads offer less impediments to terrestrial turtle movement than natural areas and thus facilitate faster transit rates. Desert tortoises sometime use washes and trails as "natural highways" according to Baxter (1988), and it is conceivable that unpaved roads would be used in a similar fashion.

While the scenario above might explain why desert tortoises construct their burrows next to roads it does not necessarily explain why so many locate their burrows under concrete pads. Desert tortoises often construct their burrows under caliche overhangs exposed in the banks of washes (Germano et al., 1994). Caliche overhangs are "hardpan" soil horizons of calcium carbonate crust that form in some desert areas. These layers cement the gravels and cobbles in the soil together, forming a matrix almost as hard as concrete. According to maps presented in a soil survey of Mesa (Soil Conservation Service, 1980), the Chuckwalla Series of soil is noncalcareous throughout and caliche layers do not occur at the locale. Desert tortoises at Mesa may take advantage of the concrete electrical transformer pads as a kind of "artificial caliche," and benefit from the roof stability that they confer. Alternatively, tortoises may associate with concrete because of its thermal inertia relative to soil. On several occasions we have observed desert tortoises "basking" on the pads on overcast mornings when the concrete was notably warmer to the touch than the surrounding soil surface.

The non-random distribution of burrows at Mesa demonstrates the importance of fine-scale habitat characteristics in modeling desert tortoise burrow locations. Some of the unexplained variation in our DFA is probably due to the fact that one tortoise may use more than one burrow over a short period of time. Burge (1978) observed tortoises using 12–25 cover sites per year, and Bulova (1994) found that desert tortoises in southern Nevada used 3–18 burrows during a five month study. At nearby Twentynine Palms, California, Duda et al. (1999) determined that the average number of burrows used per year ranged from 3.1–6.9, and differed among drought and wet years. Better models might be generated by considering individual variation in burrow use. Another source of unexplained variation may be the importance of larger-scale landscape features, as has been demonstrated for *G. polyphemus* burrow orientation by McCoy et al. (1993).

By now it is nearly axiomatic among conservation biologists working in the Mojave Desert that virtually any human alteration of habitat is deleterious to desert tortoise populations (Fish and Wildlife Service, 1994). The cumulative impacts of human activities on ecological patterns and processes in the California deserts are well documented (Lovich and Bainbridge, 1999), but still poorly understood in terms of the exact consequences to wildlife and the habitat on which they depend. While few would argue that outright habitat destruction is anathema to conservation of virtually all wild species, insufficient credible data are available to test the hypothesis that other forms of habitat alteration, or human presence, contributed to the purported decline of the desert tortoise.

While the potentially harmonious situation between desert tortoises and turbines at Mesa is more a result of serendipity than design, the results of our study suggest that certain forms of development may be compatible with conservation of species such as the desert tortoise. Our analysis suggests that the desert tortoise is more adaptable to certain anthropogenic changes in the environment than the above axiom suggests.

Most of the wind energy operations in the area prohibit or greatly restrict access by the public with locked gates, no trespassing signs, and barbed wire fences. This eliminates or greatly minimizes negative impacts associated with vandalism, illegal collection of plants and animals, off-highway vehicle use, and other human impacts (Fish and Wildlife Service, 1994; Brooks, 1999; Lovich and Bainbridge, 1999). In effect, the areas become preserves if they are large enough to meet the needs of the species living therein.

It is important to note that neutral or positive effects of wind energy development to charismatic or politically important species may not be shared by other species or their habitat. For example, wind energy development may cause increased avian mortality (Byrne, 1983; Musters et al., 1996) and increased erosion in hilly terrain (Wilshire and Prose, 1987). Therefore, we are not advocating the proliferation of wind energy development in habitats occupied by either the desert tortoise or other protected species, but rather suggest that by recognizing and planning for the needs of wildlife, the negative impacts of development can be lessened or perhaps even ameliorated.

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