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Physical and Microhabitat Characteristics of Burrows Used by Juvenile Desert Tortoises (*Gopherus agassizii*)

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ABSTRACT. – We measured the physical and microhabitat characteristics of 96 natural burrows of juvenile desert tortoises (*Gopherus agassizii*) located inside an enclosure at the Fort Irwin Study Site in the Mojave Desert, San Bernardino County, California, USA. Burrows were oriented in an east-northeasterly direction with a mean angle of orientation of 71°. Significantly more burrows were located under shrub canopies (80%) than in either the canopy margin (7%) or in open areas (13%). We found that placement of burrows under shrubs was not related to shrub availability, either by shrub abundance or percent cover. Approximately 80% of all burrows located under shrubs were underneath the canopy of two species of shrubs, *Larrea tridentata* and *Lycium pallidum*. For all shrub species combined and for *Larrea* and *Lycium* species separately, juvenile burrows were more often found under relatively large shrubs than under relatively small shrubs. Of the 59 shrubs with burrows, 17 had more than one burrow under their canopy, and in all cases these shrubs were *Larrea* or *Lycium*. We hypothesize that large shrubs may provide juveniles with more protection from predators and/or offer a more suitable microclimate than do either small shrubs or open areas. The use of specific species of larger shrubs for burrow placement by juvenile desert tortoises may be a critical factor in assessing habitat quality for tortoises, and therefore could aid in identifying criteria necessary for habitat management for this threatened species.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; juveniles; burrows; vegetation structure; microhabitat; orientation; habitat suitability; Mojave Desert; California; USA

The desert tortoise, *Gopherus agassizii*, is a long-lived, herbivorous reptile, whose range includes parts of the Mojave and Sonoran deserts of the southwestern United States and northwestern Mexico (Iverson, 1992). These desert habitats are characterized by low annual precipitation and a wide range of both daily and seasonal temperatures (Patterson, 1982; Germano et al., 1994).

Many factors such as food and water availability, reproductive requirements, and cover sites (i.e., shade resources) have been shown to be important in determining the relationship between habitat quality and the abundance, occurrence, and distribution of tortoises (Luckenbach, 1982; Schamberger and Turner, 1986). Cover sites are important to the desert tortoise for behavioral thermoregulation (Woodbury and Hardy, 1948; McGinnis and Voigt, 1971). Cover sites range from above-ground shelters to subsurface caves and burrows (Burge, 1978).

Above-ground shelters include shrubs and pallets (depressions or scrapes dug by the tortoise, normally beneath shrubs or rock overhangs and not completely covering the tortoise). Burrows are either excavated by the tortoise or another animal. Burrows provide the coolest ambient temperatures during the day and the warmest temperatures at night, and their use is a necessary component of the environment for the desert tortoise (McGinnis and Voigt, 1971; Morafka, 1982).

Because burrows of both adult and juvenile tortoises have been shown to be associated with vegetation more often than with open areas (Burge, 1978; Berry and Turner, 1986; Tom, 1994), understanding the relationships between burrows and vegetation can aid in assessing the quality of tortoise habitat, which is a necessary component of habitat management. Indeed, the habitat requirements of all life stages of a tortoise species must be understood to assess suitable habitat for tortoises (Schamberger and Turner, 1986).

Because juvenile tortoises heat and cool more rapidly than do adults, they may be more susceptible to temperature extremes than are adults (Naegle, 1976; Rose and Judd, 1982), and therefore, may be more selective regarding burrow placement or use. Microhabitat use by neonate Bolson tortoises (*Gopherus flavomarginatus*) is primarily determined by the location of their burrows (Tom, 1994). Herein, we report on the physical and microhabitat characteristics of juvenile desert tortoise burrows in order to assess the habitat requirements of this critical stage of life history.

MATERIALS AND METHODS

Study Site. — Our study was conducted at the Fort Irwin Study Site (FISS) of the U.S. Army National Training Center, San Bernardino County, California (35°06'N, 116°29'W; 650 m elevation) from October 1996 through March 1997. The vegetation is dominated by widely spaced shrubs of creosote bush (*Larrea tridentata*), burro bush (*Ambrosia dumosa*), and thornbush (*Lycium pallidum*). The site is located on a gently inclined east facing slope of alluvial origin in the central Mojave Desert. In 1989, two enclosures (FISS-I and FISS-II) measuring 60 x 60 x 2.5 m each were constructed as arenas in which behavior and physiology of juvenile desert tortoises could be studied in a semi-natural environment (Morafka et al., 1997). The enclosures, consisting of relatively undisturbed Mojave vegetation, were fenced along the sides and top to exclude predators and reinforced at ground level with small-mesh hardware cloth (buried 30 cm deep) to prevent juvenile tortoises from digging out (Hillard, 1996; Spangenberg, 1996). Since 1990, adult females have been released inside the enclosures during the spring nesting season and allowed to nest without disturbance (Joyner-Griffith, 1991; Morafka et al., 1997). Juvenile tortoises roam freely and are able to construct burrows anywhere within the enclosures. We measured the characteristics of the burrows of juveniles (neonates to 4 yrs old) in one of the enclosures (FISS-I), which is divided equally into east and west halves by a chicken wire fence reinforced at ground level with hardware cloth. At the time of our study, approximately 71 juveniles resided inside the FISS-I enclosure.

Characteristics of Burrows. — We located all burrows in the enclosure and marked each one with a numbered wooden stake placed approximately 10 cm to the right of the entrance. Physical and microhabitat characteristics were measured for each burrow. Physical characteristics included burrow compass orientation, length, width, and incline. Because a few juvenile burrows were located deep inside the canopy of a shrub, we were unable to obtain measurements of the physical characteristics of all burrows; therefore, sample sizes differ for each measurement taken.

Using a handheld compass, we measured two compass orientations in increments of five degrees for each burrow. First, we measured the magnetic compass orientation of the burrow entrance as it pointed outward. Second, for burrows located under a shrub, we measured the compass orientation from the trunk of the shrub to the burrow entrance. These two measurements gave us the direction that the mouth of the burrow faced and the orientation of the burrow to the shrub. All compass-orientation measurements were corrected from magnetic to true north.

The length of each burrow was measured using a 3 m fiberoptic cable attached to a scope (Olympus). The cable was fed down the burrow until it reached the bottom, and the length of the withdrawn cable was measured using a meter stick. The width of each burrow was measured at a length of 10 cm down the burrow (when possible) to account for possible erosion of the burrow opening. The incline of each burrow was measured in degrees from horizontal using an inclinometer placed at the burrow entrance.

The fiberoptic scope also was used to determine whether each burrow was occupied by a tortoise, and to distinguish tortoise burrows from rodent burrows, which were eliminated from the study. Tortoise burrows are characterized by having a flat floor and rounded ceiling (half-moon shaped), whereas rodent burrows are circular in cross section (Burge, 1978). We were unable to distinguish between burrows originally dug by a tortoise and those that were originally rodent burrows and subsequently modified by a tortoise.

Microhabitat characteristics for burrows were recorded as either: 1) under the canopy of a shrub, 2) within the canopy margin of a shrub, or 3) in the open. The canopy margin is defined as a narrow ring of vegetation (usually annuals) that extends a short distance beyond the edge of the shrub canopy. Based upon data from a previous study, the nearest-neighbor distance among shrubs averaged 0.8 m and the open area comprised 86% of the ground surface habitat inside the enclosure (Hillard, 1996).

To determine whether juveniles placed their burrows under a particular type (i.e., species or size) of shrub, we compared the characteristics of shrubs with burrows to those without burrows. Each shrub was identified to species, measured, and the presence or absence of burrows under its canopy was recorded. When the canopies of two or more shrubs of *different* species overlapped, they were classified as a conglomerate. When the canopies of two or more shrubs of the *same* species overlapped, they were classified as one shrub. Shrub or conglomerate size was determined by measuring the length (L), width (W), and height (H), and then computing the volume using the equation L x W x H.

To determine whether juveniles placed their burrows under shrubs based upon each species' total cover (surface area) within the enclosure, we compared the observed number of burrows located under each shrub species to the expected number of burrows (based on percent cover of each species). Although some shrubs had more than one burrow located underneath their canopy, these shrubs were used only once in all statistical analyses.

RESULTS

We located 96 juvenile tortoise burrows inside the enclosure. Juvenile tortoise burrows averaged 47.1 cm long (range 5–115 cm, SD = 29.8, $n = 89$), 6.8 cm wide (range 3–14 cm, SD = 2.3, $n = 95$), and had an average incline of 8.6° (range 2-17°, SD = 3.2, $n = 90$) from horizontal. Burrow length was positively correlated with burrow width (Least squares linear regression: $F_{(1,86)} = 31.3$, $p < 0.001$, $r^2 = 0.27$, $y = 1.21 + 6.69x$). Burrow incline also was positively correlated with burrow width ($F_{(1,88)} = 4.53$, $p < 0.05$, $r^2 = 0.05$, $y = 6.49 + 0.31x$).

The distribution of compass orientations of burrow entrances differed from a uniform distribution (Fig. 1a; Rayleigh's test (Zar, 1996): $Z = 6.35$, $n = 96$, $p < 0.001$). The mean angle of burrow mouth orientation was 71° (east-northeasterly). For those burrows located underneath a shrub canopy, the distribution of compass orientations of burrow openings from shrub trunks did not differ from a uniform distribution (Fig. 1b; $Z = 2.52$, $n = 77$, $p > 0.05$).

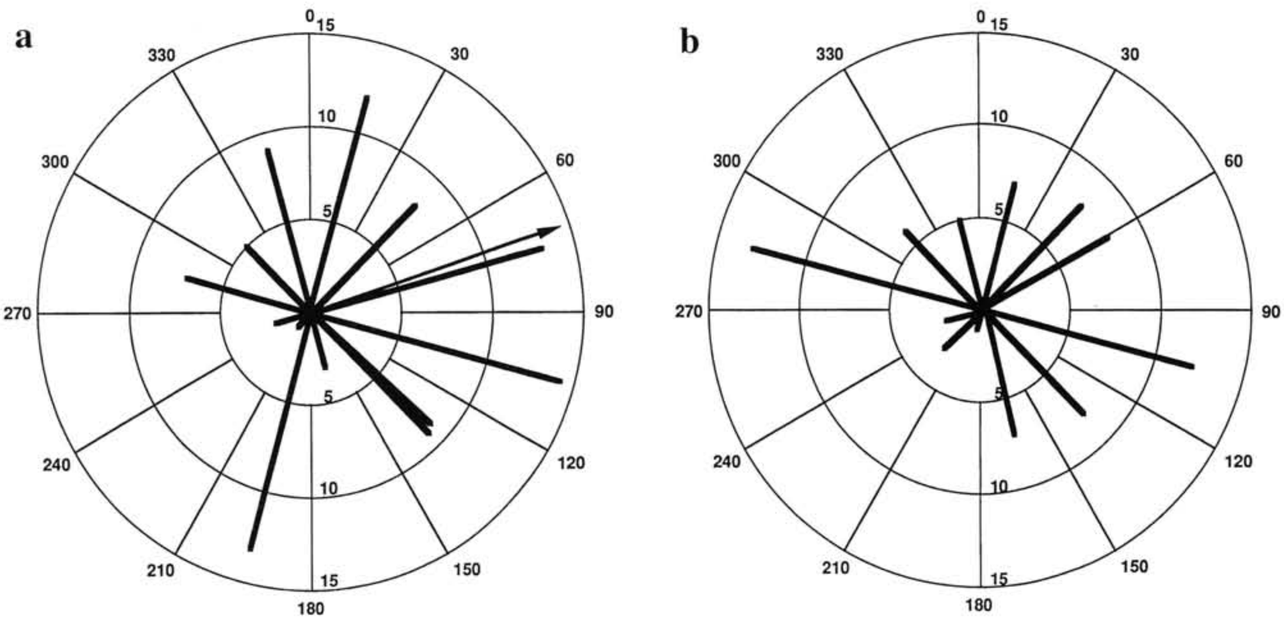

Figure 1. Frequency of compass orientations of juvenile tortoise burrow openings (**a**) pointing outward, and (**b**) in relation to shrub trunks. Arrow in figure **a** indicates mean angle of orientation (71°).

We identified to species and measured the size of 622 individual shrubs (including conglomerates) located inside the enclosure. Shrubs having the largest volumes were *Larrea tridentata* and *Lycium pallidum*, but the most numerous shrubs were *Ambrosia dumosa* (Fig. 2). Of the 96 burrows, significantly more were located under a shrub canopy (80%) than in either canopy margins (7%) or in the open (13%) (Chi-square = 95.30, df = 2, $p < 0.001$); 77 burrows were located under 59 shrubs or shrub conglomerates. The frequency distribution of shrub species with burrows was found to differ significantly from the frequency distribution of shrub species without burrows (Fig. 3; G-test of independence: $G = 117.4$, $df = 8$, $p < 0.001$). The size-class distribution of shrubs with burrows was found to differ significantly from that of shrubs without burrows (Fig. 4; Mann-Whitney U-test: $U_{59,563} = 2956.5$, $p < 0.001$).

Because 79.7% of burrows located under shrubs were located under two species of shrubs (Fig. 3; 37.3% *Larrea tridentata* and 42.4% *Lycium pallidum*), and these two species had larger mean volumes than did the other shrub species within the enclosure (Fig. 2), we compared the size-class distributions of shrubs with and without burrows for these two species separately. The distribution of shrubs with burrows differed significantly from that of shrubs without burrows for both *Larrea* (Fig. 5a; Mann-Whitney U-test: $U_{22,39} = 634.0$, $p < 0.002$) and *Lycium* (Fig. 5b; $U_{25,63} = 1206.0$, $p < 0.001$).

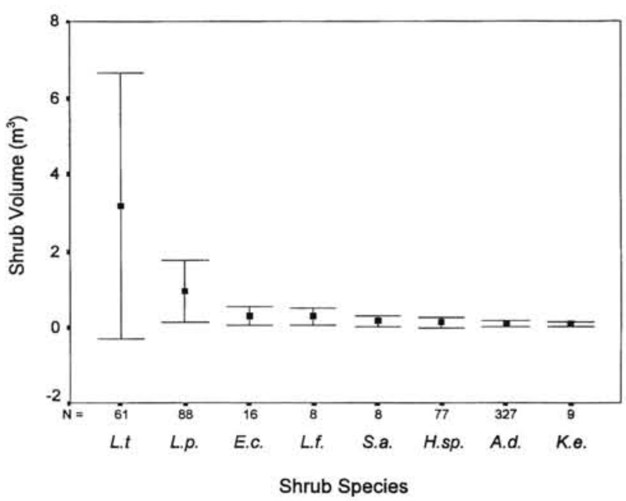

Figure 2. Estimated volume for the eight species of shrubs found inside the FISS-I enclosure (from largest mean volume to smallest, ± 1 SD). Number of individuals in the enclosure is shown below the *x* axis. L.t. = *Larrea tridentata*; L.p. = *Lycium pallidum*; E.c. = *Ephedra californica*; L.f. = *Lepidium fremontii*; S.a. = *Senna armata*; H. sp. = *Hilaria* sp.; A.d. = *Ambrosia dumosa*; K.e. = *Krameria erecta*.

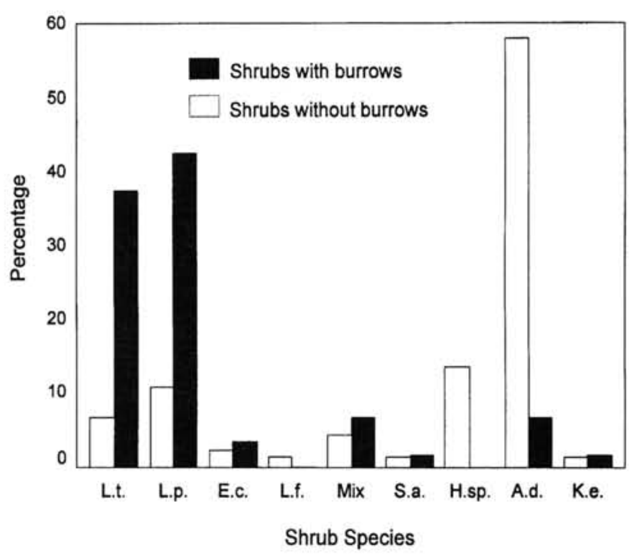

Figure 3. Percentage of each shrub species with and without juvenile tortoise burrows in the FISS-I enclosure. Abbreviations follow those in Fig. 2. Mix = conglomerates.

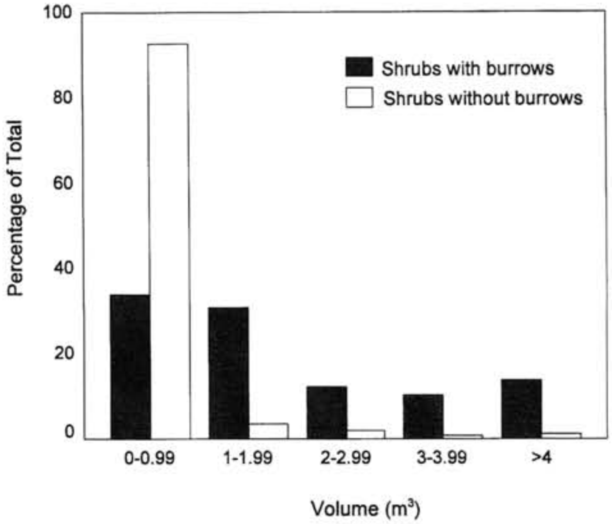

Figure 4. Distributions of size classes of shrubs with and without tortoise burrows in the FISS-I enclosure.

Of the 59 shrubs with burrows, 17 had more than one burrow under their canopies: 16 had two burrows and 1 had three burrows. Eight of these shrubs were *Larrea*, eight were *Lycium*, and one was a conglomerate of *Larrea* and *Lycium*. Shrubs with one burrow were significantly smaller in volume ($\bar{x}$ = 1.9 m^3 ± 2.7) than were shrubs with multiple burrows ($\bar{x}$ = 4.0 m^3 ± 4.2; t- test: t = 2.27, p = 0.01, df = 57).

The total surface area covered by the 622 shrubs within the 7200 m^2 enclosure was 429.9 m^2. Based on the percent cover of each shrub species within the enclosure, we found that the observed frequency of burrows located under each shrub species differed significantly from the expected frequency of burrows, assuming random burrow placement (G-test of goodness of fit: G = 20.2, $p < 0.001$, df = 3; cells < 5 were combined).

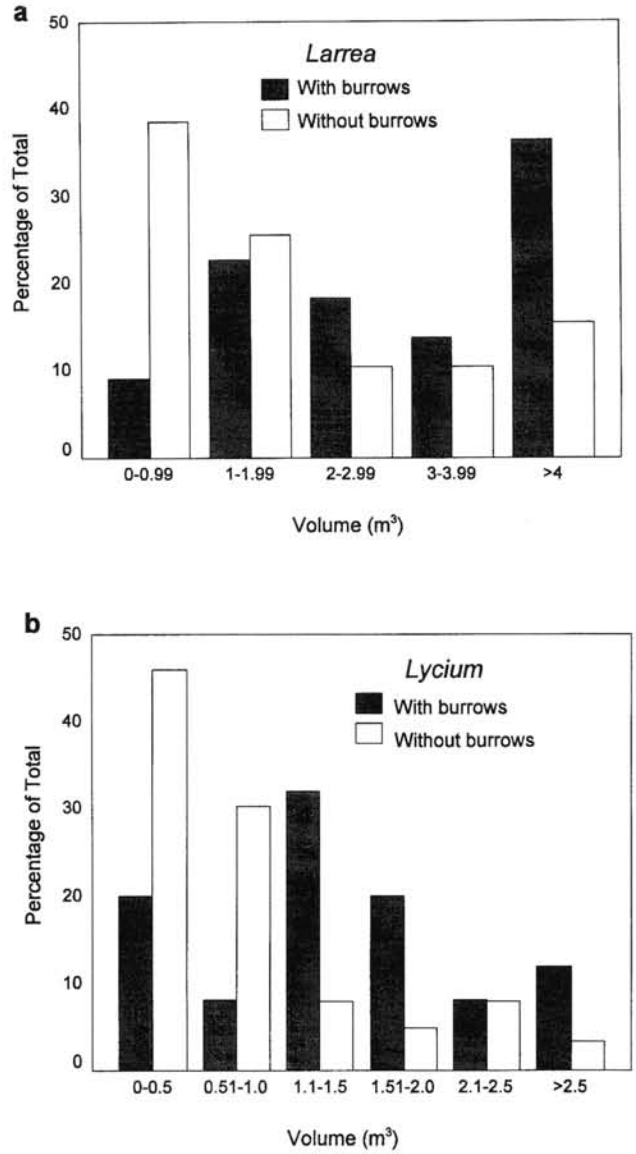

Figure 5. Distributions of size classes of *Larrea tridentata* (**a**) and *Lycium pallidum* (**b**) with and without tortoise burrows in the FISS-I enclosure.

DISCUSSION

Burrows used by juvenile desert tortoises at the study enclosure averaged 47 cm long and 6.8 cm wide. In a study in southern Nevada, juvenile tortoise burrows (n = 35) averaged 37 cm long and ranged from 5 to 9 cm wide (Burge, 1978). Burge (1978) suggested that a positive relationship existed between tortoise size and burrow width. Also, several studies on the gopher tortoise (*Gopherus polyphemus*) have shown a positive correlation between tortoise size (carapace length) and burrow width (see Wilson et al., 1991). We found a weak, but significant, positive correlation between burrow width and burrow length. If we assume a positive relationship between tortoise size and burrow width, it appears that larger juveniles dig relatively longer burrows than do smaller juveniles.

The openings of the burrows generally oriented in an east to northeasterly direction with a mean angle of orientation of 71°. Burge (1978) measured the orientation of desert tortoise burrows in southern Nevada, but analyzed burrows located under shrubs separately from those located in open areas. To make her data comparable to ours, we combined Burge's (1978: Table 2) data for burrows located under shrubs and in the open, reanalyzed them using Rayleigh's test for circular distributions, and computed a mean angle of orientation for all burrows. Similar to our results, burrows in Burge's southern Nevada population oriented in a north to northeasterly direction with a mean angle of orientation of 41°. Burge (1978) speculated that a burrow facing in this direction may be at a thermal advantage in the summer months because the opening would only receive direct sunlight during the morning hours. Additionally, juveniles may orient the opening of their burrows in east to northeasterly directions because the rays of the morning sun may visually arouse tortoises (before temperature cues), fostering early morning activity such as foraging for succulent vegetation. In contrast, Berry and Turner (1986) found that in several California populations of desert tortoises, significantly more juvenile burrows opened to westerly to southeasterly directions. Differences in burrow orientations between studies could be attributable to one or a combination of factors. First, Burge (1978) measured the orientation of 619 burrows, of which only a small percent were juvenile burrows (≤ 5.7%); hence, the observed pattern was biased heavily towards adult burrows. Second, Berry and Turner (1986) combined data on juvenile burrow orientation from 18 study sites. Burrow orientation may be site specific, and therefore, may vary as a result of latitude, elevation, and/or other topographic features of the landscape (McCoy et al., 1993).

Significantly more burrows were located under the canopy of shrubs than in the canopy margin or in the open. Burrow placement by juvenile tortoises under shrub canopy was independent of shrub species abundance. Although 37.3% of burrows were located under *Larrea tridentata* and 42.4% under *Lycium pallidum*, these shrubs comprised only 6.7% and 10.8%, respectively, of shrubs within the enclosure. The majority of shrubs within the enclosure were *Ambrosia dumosa* (58.0%), however, only 6.8% of burrows were located under this species. The disparity in use of shrub species relative to their abundance appears to be a consequence of shrub size. Juveniles placed more burrows under larger shrubs than under smaller shrubs. Although individual *Larrea* and *Lycium* are, on average, larger in surface area than are the other shrub species within the enclosure, more juvenile burrows were found underneath the canopy of larger individuals than smaller individuals of these two species.

Other investigators have shown that burrows used by juvenile tortoises are more often placed under shrub canopies than in open areas (Burge, 1978; Berry and Turner, 1986). In California, juvenile desert tortoises placed the majority of their burrows under woody shrubs with 59% of burrows under *Larrea* (Berry and Turner, 1986). In southern Nevada, adult and juvenile cover sites (burrows and pallets) were more often found under shrub canopies (72%) than in open areas (Burge, 1978). As in this study, Burge (1978) found no correlation between the use of a shrub species for burrow placement and that species' abundance in the habitat, indicating that tortoises favored some shrub species over others. Although Burge (1978) did not directly correlate shrub use with shrub size, she did suggest that a relationship existed between burrow placement and the "shade-giving properties" of a shrub species. In a study of hatchling Bolson tortoises, more burrows were located in shrub/cacti microhabitats than in grass, and none were found in open areas (Tom, 1994).

Juvenile tortoises spend most of their time inside their burrows during all seasons (Wilson et al., 1994; Hillard, 1996), and above-ground activity usually is centered around the burrow (e.g., Tom, 1994; Wilson et al., 1994; Hillard, 1996). The placement of burrows under shrub canopies versus open areas may offer juvenile tortoises increased protection from predators (Tom, 1994). Hatchling Bolson tortoises placed the majority of their burrows under the cactus *Opuntia*, whereas in our study, most burrows were placed under the box thorn *Lycium* and creosote bush *Larrea*. *Opuntia* and *Lycium* have sharp spines, which may offer protection for juveniles from predators. The use of relatively large shrubs also may afford added protection to juveniles from predators by providing a larger surface area of ground shielded by shrub canopy for daily activity.

Additionally, shrub canopy may offer a more suitable microclimate for juvenile tortoises than do open areas (Tom, 1994). In summer, the coolest microsites available to juveniles in the enclosure are located in the shade of shrubs, whereas the hottest microsites are located on the sunny side of shrubs because of restricted air movement (Hillard, 1996). Juvenile tortoises, therefore, have available to them a wide range of microclimates within the confines of the shrub canopy. Burrows located under shrub canopies also have higher relative humidity levels than do those at open sites (DSW, unpubl. data). In areas that are heavily grazed, shrubs may offer burrows added protection from damage by domestic animals (Nicholson and Humphreys, 1981). Finally, because of the root mass, the soil under shrubs may increase the structural integrity of burrows, allowing them to persist longer than they would in open areas.

Habitat destruction is one of the primary factors implicated in the decline of the desert tortoise throughout its range (U.S. Fish and Wildlife Service, 1994). Human activities that reduce shrub cover may limit the amount of suitable habitat available to juvenile tortoises. Both off-road vehicle use and grazing by cattle and sheep have been shown to reduce plant cover (Luckenbach, 1982). Population studies of two Mediterranean tortoise species concluded that, although variation existed among populations, fewer juveniles were present at sites that had been disturbed (Hailey et al., 1988). In Argentina, active burrows of subadult and adult *Geochelone chilensis* were most often associated with shrubs (specifically *Larrea* spp.) in ungrazed areas, whereas active burrows were not detected in areas with livestock grazing (Waller and Micucci, 1997). Although many habitat variables already have been shown to affect habitat quality (e.g., rainfall, soil type, elevation; Schamberger and Turner, 1986), more information is required to fully understand the complexity of the relationship between shrub size and density, and the presence and abundance of juvenile tortoises.

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