# Habitat Use by Desert Tortoises (*Gopherus agassizii*) on Alluvial Fans in the Sonoran Desert, South-Central Arizona

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**Desert Tortoises (*Gopherus agassizii*) in the Sonoran Desert typically occur on rocky slopes and bajadas and are absent from intermountain valley floors. Tortoises also occur along deeply incised washes emanating from rocky bajadas, using caliche caves as shelter sites. The Florence Military Reservation (FMR), in south-central Arizona, is typified by gently sloping alluvial fans bisected by steeply incised washes. One 10.9-ha hill consisting of volcanic outcrops and boulders occurs at the northern end of the reservation. Tortoise locations at FMR were concentrated around incised washes with dense caliche caves or near the volcanic hill. Home ranges of male and female tortoises were not significantly different, and the sexes used shelter types similarly. Tortoises used caliche caves as shelter more than other shelter types, especially those tortoises without access to the rocky hill. Compositional analysis of the three principal habitat types used by tortoises at FMR revealed that they selected incised washes over the other habitat types. However, we did not find tortoises in washes with few caliche caves. These results suggest that availability of shelter sites strongly influences tortoise distribution at FMR.**

THE Desert Tortoise (*Gopherus agassizii*) has the broadest range of latitude and habitats of the four species of North American tortoises (Germano et al., 1994; Berry et al., 2002). Throughout the Mojave Desert, tortoises occur on sandy loam to rocky soils on valley bottoms and bajadas and occasionally on rocky hillsides (Germano et al., 1994; Berry et al., 2002). In both the Lower Colorado River Valley and Arizona Upland subdivisions of the Sonoran Desert in Arizona, tortoises typically occur on rocky slopes and bajadas and are absent from intermountain valley floors (Barrett, 1990; Van Devender, 2002). Tortoises at the southern end of their distribution in Sinaloan thornscrub and deciduous forest have only been documented on hillsides (Fritts and Jennings, 1994).

Desert tortoises use shelters extensively throughout their range (Germano et al., 1994), spending up to 95% of their life within a shelter due to extreme environmental conditions (Nagy and Medica, 1986). In the Mojave Desert, burrows are generally constructed in soil, near the base of shrubs, or in wash banks (Luckenbach, 1982). In the Sonoran Desert, tortoises use a wide variety of substrates for shelter. In more typical habitat, they primarily shelter under rocks, but they commonly use woodrat middens, burrows dug by other animals, or caliche caves exposed in the incised banks of washes (Averill-Murray et al., 2002a; Van Devender, 2002).

Desert tortoises use burrows as shelter from temperature extremes (Zimmerman et al., 1994; Bailey et al., 1995; Rautenstrauch et al., 1998, 2002), as well as for predator avoidance, courtship, and nesting (Averill-Murray, 2002; Duda et al., 2002). In addition, tortoises also exhibit high burrow-use fidelity, using known travel paths (Berry, 1986; Duda et al., 2002) and returning to the same hibernacula or nest sites in successive years (Averill-Murray et al., 2002a, 2002b).

Little is known about the low-density tortoise populations found below the rocky slopes and bajadas of desert mountain ranges in the Sonoran Desert (Averill-Murray and Averill-Murray, 2005). Use of caliche caves or densely packed woodrat middens contributes to the cryptic nature of these tortoise populations and makes them difficult for researchers to locate (Van Devender, 2002). From 2000 to 2004 we examined habitat use by one of these cryptic populations of Desert Tortoises on and around alluvial fans radiating from the west side of the Mineral and Tortilla mountains in Pinal County, Arizona. The goal was to better understand how tortoises use this marginal habitat. Our primary null hypothesis was that tortoises, of both sexes, use available habitat types equally within the study area.

## MATERIALS AND METHODS

The study site was located on the Florence Military Reservation (FMR), a 10,421-ha site located 80 km southeast of metropolitan Phoenix. Snetsinger and Spicer (2001) described the physiography and vegetative associations of the site. Florence Military Reservation contains both the Arizona Upland and Lower Colorado River Valley subdivisions of the Sonoran Desert (Brown, 1994). Three major biomes (Sonoran Desertscrub, Sonoran Riparian Scrubland, and Sonoran Interior Strand) occur within those two subdivisions on the FMR. The geology is characterized by gently sloping to flat alluvial fans in the north that have been mostly filled in by unconsolidated to weakly consol-

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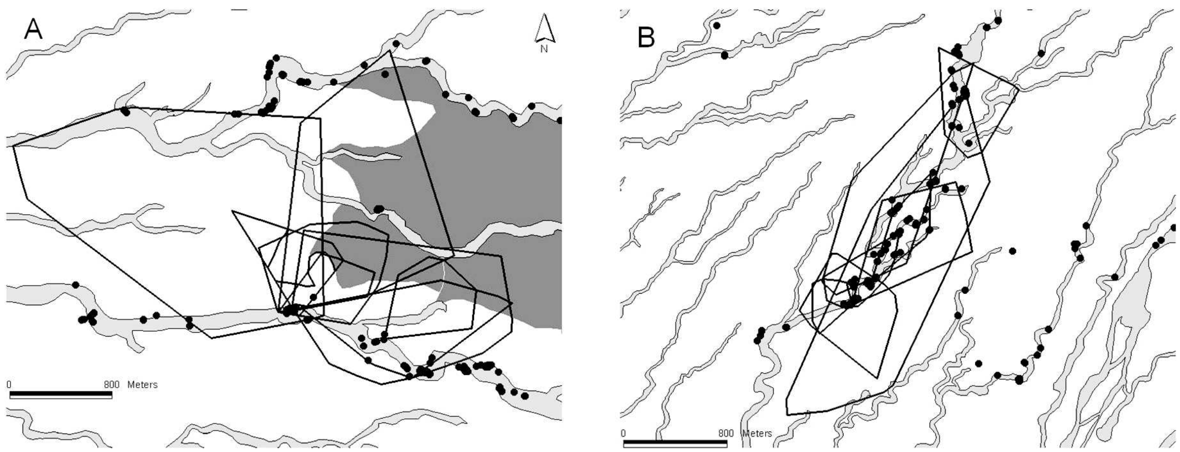


**Fig. 1.** Desert tortoise minimum convex polygons and caliche cave locations for the northern telemetry group (A) and southern telemetry group (B) overlaid on vegetation associations at Florence Military Reservation. Vegetation association A is represented by the white background in the figure. Vegetation association B is represented by the dark gray shading, and vegetation association C by the dendritic shaped, light gray coloration.

idated silts, sands, clay, and gravel from the Mineral and Tortilla mountains to the east. The alluvial fans are bisected by deeply incised washes on the eastern portion of the reservation. Our primary study area was the 4,527-ha northern portion of FMR, which included a single 10.9-ha volcanic hill.

From 2000 to 2004, we searched areas in which tortoises might occur within FMR, concentrating on sites suitable for burrow excavation, especially including incised washes with caliche caves and the volcanic hill. We also searched all washes within the study area, whether incised or not, and spent considerable time on the alluvial fans. We use the term "burrow" to specifically refer to a subsurface cavity formed by erosion or excavated by a tortoise or another animal (Burge, 1978), including cavities eroded or excavated into hard calcium carbonate (caliche) soils along incised wash banks. We use the term "shelter" more generally as any cover used by a tortoise, including burrows. We marked burrows in which we observed tortoises with individually numbered aluminum tags. We only marked relatively permanent burrows, defined as modified shelters $\geq$1/2 the tortoise's shell length. We did not mark pallets (shallow, scraped out areas $<$1/2 tortoise length) or other temporary shelters unmodified by the tortoise (for example, under trees, shrubs, or rocks). We mapped locations of all caliche caves large enough to shelter a tortoise $\geq$180 mm MCL.

For each tortoise found, we recorded midline carapace length (MCL) to the nearest mm with pottery calipers and a metal rule. We assigned each tortoise a number and permanently notched marginal scutes with triangular files using a modified system from Cagle (1939). We also wrote the identification number on a dot of correction fluid painted on the right fourth costal scute and covered it with clear epoxy. These numbers were readable throughout the course of the study. We determined sex for tortoises $\geq$180 mm MCL by considering those with concave plastrons to be males (Germano, 1994). We attached radio transmitters (ATS, AVM Instrument Company, Telonics, or Wildlife Materials) to the anterior carapace of adult tortoises using five-minute gel epoxy. During the winter months (November through February) when tortoises were inactive, we located tortoises once a week. During the activity season (March through October) we located tortoises 2–3 times a week, obtaining both morning and evening locations. We handled all tortoises with disposable latex gloves to minimize the potential spread of pathogens between individual tortoises. We disinfected any instruments coming into contact with a tortoise during handling with chlorhexidine diacetate (Nolvasan®) prior to use on another tortoise. We only handled tortoises to obtain morphometric data during initial capture, in order to attach or replace a radio transmitter, or to palpate or radiograph gravid females (reproductive data not presented). We recorded tortoise positions with Garmin GPS III Plus (Garmin Corporation) receivers and mapped the locations with Arc View GIS 3.2 (Environmental Systems Research Institute, Inc.). We divided the 18 tortoises tracked with radio telemetry into two groups relative to proximity to the 10.9-ha volcanic hill. The northern group contained nine tortoises and occurred near the hill. The southern group also contained nine tortoises, all of which occurred along incised washes and alluvial fans with no adjacent rocky habitat.

We calculated minimum convex polygon (MCP) home ranges for telemetered tortoises with the Animal Movement extension to ArcView (Version 1.1., P. N. Hooge and B. Eichenlaub, Animal Movement extension to ArcView. U.S. Geological Survey, Alaska Biological Science Center, Anchorage, 1997). We compared home range size among groups and sexes with ANCOVA, using total number of observations for each tortoise as a covariate (Systat 8.0, SYSTAT Software, Inc.). We compared observed shelter use among sexes and groups with ANOVA, using Type IV sums of squares to account for the lack of boulder burrows in the southern group (SPSS 14, SPSS, Inc.). Individual tortoises were nested within the group*sex interaction term. We conducted *post hoc* comparisons with Tukey's Honestly Significant Difference Test using estimated marginal means (Zar, 1984).

We overlaid tortoise locations and home range polygons on a vegetation map in ArcView (resolution to the series level of Brown et al., 1979) prepared for FMR by Snetsinger and Spicer (2001; Fig. 1). We identified three major habitat types (labeled A, B, and C) based on geomorphology and vegetation association within the study area. Habitat A was characterized by flat to gently sloping alluvial fans. The vegetation within habitat A consisted of no overstory and a midstory dominated by Triangle Leaf Bursage (*Ambrosia*

**Table 1.** Number of Radio Telemetry Locations, Minimum Convex Polygon (MCP) Home Range Areas, and Relative Shelter Use by Type for Desert Tortoises at Florence Military Reservation. Shelters include all observations among the described shelter types and may include multiple observations within unique shelters.

| | | MCL | MCP | | Shelters | Caliche Cave | Soil Burrow | Pallet | Woodrat Midden | Boulder Burrow |
|---|---|---|---|---|---|---|---|---|---|---|
| ID# | Sex | mm | ha | *n* | *n* | % | % | % | % | % |
| Southern Group | | | | | | | | | | |
| 400 | M | 204 | 23.5 | 215 | 180 | 80 | 3 | 9 | 8 | – |
| 403 | M | 277 | 93.4 | 210 | 172 | 50 | 32 | 7 | 11 | – |
| 406 | M | 248 | 9.7 | 221 | 204 | 97 | 0 | 3 | 0 | – |
| 411 | M | 240 | 9.0 | 156 | 143 | 97 | 1 | 2 | 1 | – |
| 404 | F | 264 | 28.1 | 232 | 183 | 82 | 0 | 17 | 1 | – |
| 405 | F | 232 | 5.1 | 229 | 178 | 45 | 2 | 6 | 47 | – |
| 410 | F | 250 | 46.2 | 177 | 149 | 83 | 3 | 12 | 3 | – |
| 412 | F | 246 | 17.4 | 222 | 184 | 65 | 22 | 11 | 1 | – |
| 502 | F | 217 | 12.0 | 223 | 158 | 32 | 45 | 9 | 14 | – |
| Mean | | 242.0 | 27.2 | 209.4 | 172.3 | 70.1 | 12.0 | 8.4 | 9.6 | – |
| SD | | 22.36 | 27.86 | 25.75 | 19.22 | 23.36 | 16.81 | 4.64 | 14.92 | |
| Northern Group | | | | | | | | | | |
| 413 | M | 243 | 43.1 | 188 | 164 | 43 | 5 | 4 | 48 | 0 |
| 414 | M | 246 | 29.1 | 142 | 112 | 32 | 0 | 5 | 56 | 6 |
| 419 | M | 229 | 25.7 | 191 | 140 | 36 | 19 | 7 | 10 | 29 |
| 408 | F | 229 | 5.0 | 30 | 18 | 50 | 44 | 0 | 0 | 6 |
| 420 | F | 245 | 11.2 | 216 | 179 | 12 | 16 | 13 | 41 | 18 |
| 421 | F | 232 | 3.1 | 139 | 117 | 31 | 0 | 3 | 0 | 66 |
| 430 | F | 185 | 10.0 | 124 | 95 | 37 | 6 | 16 | 0 | 41 |
| 503 | F | 206 | 5.5 | 110 | 81 | 6 | 64 | 12 | 0 | 17 |
| 501 | F | 198 | 52.8 | 58 | 96 | 3 | 23 | 7 | 66 | 1 |
| Mean | | 223.7 | 20.6 | 133.1 | 111.3 | 27.8 | 19.7 | 7.4 | 24.6 | 20.4 |
| SD | | 22.14 | 18.10 | 61.48 | 47.88 | 16.75 | 21.67 | 5.22 | 27.73 | 21.80 |

*deltoidea*). Habitat A also contained Creosote Bush (*Larrea tridentata*) and a scattered mix of cacti including Chainfruit Cholla (*Opuntia fulgida*), Buckhorn Cholla (*Opuntia acanthocarpa*), Brownspine Prickly Pear (*Opuntia phaecantha*), and Engelmann Prickly Pear (*Opuntia engelmanii*). Habitat B was distinguished by volcanic outcrops and boulders that comprise a solitary volcanic hill in the northeast corner of the reservation. Vegetation in habitat B was a complex of the Creosote Bush–Triangle Leaf Bursage–mixed cacti–(lowland) mixed scrub association and the Triangle Leaf Bursage–mixed cacti–(lowland) mixed scrub association. Triangle Leaf Bursage dominated the side slopes, and Creosote Bush occurred along the ridge top. Habitat C consisted of incised washes, which we characterized as xeroriparian, a habitat periodically submerged and dominated by an overstory of Paloverde (*Parkinsonia microphylla*), Desert Ironwood (*Olneya tesota*), and Velvet Mesquite (*Prosopis velutina*).

We used compositional analysis (Aebischer et al., 1993; Pendleton et al., 1998; Gabor and Hellgren, 2000) to determine habitat use based on MCP home range. Compositional analysis takes into account that each individual's movements determine a trajectory through space and time, and habitat use is the proportion of that trajectory contained within each habitat type. We calculated the proportion of each habitat type within each home range polygon and calculated the proportion of each tortoise's observed locations in each habitat. We performed log-ratio transformations on the resulting proportions. We used the log-ratio differences between habitat types to determine habitat selection by tortoises. The matrix of mean log-ratio differences of habitat use by tortoises at FMR will either display negative values denoting selection against a certain habitat or positive values representing selection for a certain habitat. We then ranked habitat types by adding the number of positive values associated with each habitat type, with the type having the highest value being the one selected by the tortoise. If the individual is using each habitat in direct relation to its availability, we conclude that animals do not select for any habitat type. We analyzed these data using Resource Selection Analysis Software (F. Leban, Resource Selection For Windows 1.00b8.4. University of Idaho, Moscow, 1999. http://www.cnrhome.uidaho.edu/fishwild/Garton/tools). All means are reported ± 1 standard deviation.

## RESULTS

We spent a total of 465 person-field days searching for and monitoring tortoises and mapping the locations of 597 caliche caves. We marked 37 tortoises (ten males, 20 females, and seven juveniles) and recorded 3,132 tortoise locations. We followed the movements of up to 18 tortoises: seven males, eleven females. There were differences in numbers of tortoises followed between years because of tortoise mortality ($n = 3$), early transmitter failure ($n = 1$), and addition of new individuals throughout the progression of the project.

**Table 2.** Proportional Habitat Available in Each Desert Tortoise MCP and Used (as Determined by Radio Telemetry Locations) at Florence Military Reservation. Habitats are: A = gently sloping or flat alluvial slopes; B = volcanic hills; and C = incised washes.

| | | Habitat | | | | | |
|---|---|---|---|---|---|---|---|
| | | A | | B | | C | |
| Tortoise # | Sex | Available | Used | Available | Used | Available | Used |
| Southern Group | | | | | | | |
| 400 | M | 0.91 | 0.33 | 0 | 0 | 0.09 | 0.67 |
| 403 | M | 0.87 | 0.81 | 0 | 0 | 0.13 | 0.29 |
| 404 | F | 0.80 | 0.28 | 0 | 0 | 0.20 | 0.72 |
| 405 | F | 0.82 | 0.82 | 0 | 0 | 0.18 | 0.18 |
| 406 | M | 0.70 | 0.26 | 0 | 0 | 0.30 | 0.74 |
| 410 | F | 0.83 | 0.36 | 0 | 0 | 0.17 | 0.64 |
| 411 | M | 0.69 | 0.10 | 0 | 0 | 0.31 | 0.90 |
| 412 | F | 0.69 | 0.28 | 0 | 0 | 0.31 | 0.72 |
| 502 | F | 0.77 | 0.82 | 0 | 0 | 0.23 | 0.18 |
| Mean | | 0.79 | 0.45 | — | — | 0.21 | 0.51 |
| SD | | 0.080 | 0.283 | | | 0.080 | 0.293 |
| Northern Group | | | | | | | |
| 408 | F | 0.76 | 0.53 | 0.22 | 0.27 | 0.02 | 0.20 |
| 413 | M | 0.83 | 0.61 | 0.03 | 0.02 | 0.14 | 0.38 |
| 414 | M | 0.65 | 0.54 | 0.26 | 0.21 | 0.09 | 0.25 |
| 419 | M | 0.50 | 0.44 | 0.37 | 0.32 | 0.13 | 0.24 |
| 420 | F | 0.55 | 0.31 | 0.23 | 0.25 | 0.21 | 0.44 |
| 421 | F | 0.24 | 0.04 | 0.73 | 0.70 | 0.03 | 0.26 |
| 430 | F | 0.37 | 0.27 | 0.59 | 0.56 | 0.04 | 0.18 |
| 501 | F | 0.83 | 0.66 | 0.01 | 0.03 | 0.15 | 0.31 |
| 503 | F | 0.54 | 0.46 | 0.36 | 0.26 | 0.09 | 0.27 |
| Mean | | 0.59 | 0.43 | 0.31 | 0.29 | 0.10 | 0.28 |
| SD | | 0.203 | 0.194 | 0.236 | 0.221 | 0.063 | 0.084 |

We estimated tortoise home range sizes up to 93.4 ha (Table 1). Mean home range for males (33.4 ha ± 28.96 SD) was twice that of females (17.8 ha ± 17.23 SD), but differences were not significant according to sex ($F_{1,13}$ = 1.836, $P$ = 0.199), group ($F_{1,13}$ = 0.339, $P$ = 0.570), group*sex ($F_{1,13}$ = 0.188, $P$ = 0.672), or number of observations ($F_{1,13}$ = 0.238, $P$ = 0.634).

We marked 125 permanent shelter sites at FMR. Individual tortoises used 6–16 different burrows during the study, including 70 of the 597 mapped caves. Tortoises used five basic types of shelter at FMR: caliche caves (49% of observations ± 29.4%), woodrat (*Neotoma albigula*) middens (17 ± 22.9%), soil burrows (16 ± 19.2%), burrows under boulders (10 ± 18.3%), and pallets (8 ± 4.8%; Table 1). We found the two groups using types of shelters differentially (group*shelter $F_{3,52}$ = 12.407, $P$ = 0.000). This was primarily due to the lack of boulder shelters available to the southern group. As a result, we found those tortoises in caliche caves (mean = 70.1 ± 23.36%) more often than tortoises in the northern group (27.8 ± 16.75%; $q_{8,72}$ = 9.968, $P < 0.001$; Table 1). Use of woodrat middens, pallets, and soil burrows was similar between groups (Table 1). Males and females used shelter types similar to each other (sex*shelter $F_{4,52}$ = 2.000, $P$ = 0.133).

Caliche caves were associated with deeply incised washes, whereas soil burrows were generally found along stretches of a wash with more gently sloping sides. On a single occasion a male used a soil burrow constructed on a flat bench between two washes. Burrows under boulders only occurred on the volcanic hill in the northern telemetry area. Pallets and unmodified resting sites were usually located on alluvial slopes under shrub clumps, primarily triangle leaf bursage. Tortoises also used pallets under dead and fallen woody debris.

In the southern group, habitat A dominated most tortoises' home ranges (0.79 ± 0.08), compared to habitat C (0.21 ± 0.08; Table 2; Fig. 1B). Based on radio-telemetry observations, tortoises actually used habitat A (0.45 ± 0.28) and habitat C (0.54 ± 0.31) approximately equally (Table 2). However, because habitat A is more common at FMR, equal

**Table 3.** Matrix of Mean Log-Ratio Differences of Habitat Use by Desert Tortoises at Florence Military Reservation. Significant differences ($P$ < 0.05) between habitat types indicated by an asterisk. Ranking is assigned by counting the number of positive values in each row. Habitats are defined as: A = gently sloping or flat alluvial slopes; B = volcanic hills; and C = incised washes.

| Habitat | A | B | C | Ranking |
|---|---|---|---|---|
| Southern group | | | | |
| A | | | −1.6349* | 0 |
| C | 1.6349* | | | 1 |
| Northern group | | | | |
| A | | −0.4727 | −1.6906* | 0 |
| B | 0.4727 | | −1.2179* | 1 |
| C | 1.6906* | 1.2179* | | 2 |

**Table 4.** Number of Permanent Shelter Sites, by Cover Type, in Each Habitat.

| | Habitat type | | |
|---|---|---|---|
| Cover type | A | B | C |
| Boulder | 0 | 22 | 0 |
| Caliche | 0 | 0 | 71 |
| Midden | 5 | 0 | 0 |
| Soil | 8 | 5 | 14 |

use means preference for habitat C ($\chi^2_1 = 10.0822$, $P < 0.05$; Table 3).

In the northern group, habitat A again dominated most tortoises' home ranges (0.58 ± 0.20), followed by habitat B (0.31 ± 0.24) and habitat C (0.10 ± 0.06; Table 2; Fig. 1A). Even though habitat B exceeded habitat C by three times, tortoises used the two types approximately equally (Table 2). Tortoises selected habitat C over habitat A and habitat B ($\chi^2_2 = 13.2413$, $P < 0.05$), but selection of habitat B over habitat A was not significant ($P > 0.05$; Tables 2–3). A review of the 125 permanent tortoise shelter sites shows the majority of shelters occurring in habitats B and C (Table 4). At least as far as shelter is concerned, tortoises are selecting more for geology than vegetation association.

## DISCUSSION

Distance-based analyses have been increasingly considered for use in habitat selection studies (Conner et al., 2003) because of advantages, compared to classification-based (e.g., compositional) analyses, in Type I error rates (Bingham and Brennan, 2004) and the ability to detect preferences for edges or other linear or point features (Conner et al., 2003). The effects of habitat patch size, shape, and distribution on both types of analyses have been debated (Conner et al., 2005; Dussault et al., 2005). However, the relatively simple landscape in our study (only three distinct habitat types) allowed us to avoid analytical pitfalls. We successfully controlled for inflated Type I error, caused by available habitat types not used by some animals, by separating the site into two areas within which each habitat type was used by every individual tortoise. At the scale of third-order selection (Johnson, 1980) in which we were interested, juxtaposition of habitat types also had no apparent confounding effects. Selection for linear features such as washes might have been obscured by compositional analysis (Conner et al., 2003), but the focal use of caliche caves as shelter within these washes led to clear results of selection. Questions involving more complex landscapes or more subtle selection for linear or point habitat features may be more conducive to a distance-based analysis.

Due to conventional wisdom that Desert Tortoises in the Sonoran Desert do not typically inhabit valley floors outside of washes (Germano et al., 1994; Van Devender, 2002), we expected to find tortoises using relatively linear home ranges along the washes as they moved between caliche caves. We found that tortoise locations coincided largely with caliche caves, particularly within the southern telemetry group where boulder cover-sites are absent. As expected, distribution of tortoise locations was either linear, following the washes themselves, or was concentrated on one small stretch of wash with a large number of caliche caves. However, we also found telemetered tortoises spending substantial time within bursage-dominated habitat on the alluvial slopes above the washes, with a few individuals spending a majority of time here (including adults of both sexes). During periods of moderate temperatures, resting tortoises were often found under bursage clumps in an unmodified shelter or a shallow, scraped-out pallet. Several tortoises spent long periods of inactivity (hibernation and hot dry periods) on benches between washes in woodrat middens.

We found that tortoises selected incised washes over other habitat types. However, tortoises used all habitat types, and all habitats provided shelter sites. Tortoise home ranges were largely centered around washes and their associated caliche caves. Tortoises with access to the volcanic hill selected that habitat in proportion to its availability, finding shelter in boulder burrows. Woodrat middens appeared to be an important shelter substrate when tortoises used the alluvial slopes. Brown (1968) found that woodrat middens offer considerable protection from the extremes of daily ambient temperatures and provide higher relative humidity. We also observed vegetative (both fresh and dead) materials packed into the entrances of caliche caves by woodrats. Although caliche caves are already insulated (Woodbury and Hardy, 1948), these vegetative materials would further dampen temperature and humidity extremes.

Desert Tortoise movement patterns at FMR, and as reported at other locations (O'Connor et al., 1994; Duda et al., 2002), often consist of a period of time spent around a burrow or group of burrows before moving to another area, thus resulting in multiple, sometimes distant, centers of activity. Tortoises alternate between several different burrows, occupying each burrow for anywhere between several minutes to several weeks. In areas where several tortoise home ranges overlap, one burrow may be used by multiple tortoises. For instance, five different radio-marked tortoises (three males, two females) made use of the same caliche cave. On 24 October 2001, three of the five tortoises (two males, one female) occupied this cave at the same time. Observed home ranges in this study generally fell within ranges observed at other populations in the Sonoran (Barrett, 1990; Averill-Murray et al., 2002a) and Mojave deserts (Burge, 1977; O'Connor et al., 1994; Duda et al., 1999). Most short-term studies of this long-lived species have apparently lacked the power to detect differences in home range size between the sexes, but Averill-Murray et al. (2002a) found that males had larger mean home ranges than females in a combined analysis of five Sonoran Desert populations.

While we were interested in overall patterns of habitat use and shelter selection and did not investigate seasonal or annual differences, habitat and shelter use may vary temporally. Desert Tortoises in the south-central Mojave Desert in California had smaller home ranges, used fewer burrows, and were less active in years of drought (Duda et al., 1999; Freilich et al., 2000). Desert Tortoises in a northern Mojave Desert population in Nevada used burrows more often during the hottest and coldest months and used pallets or were found outside of shelter more often during moderate seasons. Males used deeper burrows more often overall, used fewer burrows in spring, and used more burrows in summer and fall than females, with seasonal differences between the sexes probably related to the annual reproductive cycle (Rautenstrauch et al., 2002).

Averill-Murray and Averill-Murray (2005) found Desert Tortoises or their sign on 25% of transects surveyed below rocky bajadas, up to 1.7 km away from the nearest slope. They concluded that tortoises do occur at low density in inter-mountain valleys in the Sonoran Desert. As land and wildlife managers in the Sonoran Desert develop and implement conservation actions for Desert Tortoises, they should also consider low-density populations on lower alluvial slopes of desert mountain ranges. Development of these low-lying habitats may have a greater effect on tortoise populations than we realize (Howland and Rorabaugh, 2002). In addition to direct impacts on tortoises themselves, individuals on the periphery of mountain slopes and bajadas may represent linkages between disjunct ''rock-pile'' populations, including immigrating or emigrating individuals responsible for gene flow between tortoise populations (Edwards et al., 2004; Averill-Murray and Averill-Murray, 2005).

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