Journal of Herpetology, Vol. 38, No. 3, pp. 443–447, 2004

Characteristics of Burrows Used by Juvenile and Neonate Desert Tortoises (*Gopherus agassizii*) during Hibernation

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Abstract.—**Behavior of young tortoises released from seminatural nurseries could be affected by the length of time spent within the nursery before release. We tested whether neonate (under two months) and juvenile (8–9 years) Desert Tortoises selected hibernation burrows with differing characteristics after release from their natal pen. Burrow habitat (canopy cover and landscape slope) did not differ between age classes. Juvenile tortoises were larger than neonates and, therefore, used larger burrows than neonates, but their burrows were a closer fit to tortoise size than were the neonate burrows. Juvenile burrow orientation differed significantly from a uniform distribution, with a mean direction of 162° (SSE); the burrows of neonates were not oriented in any particular direction. Selectivity of juveniles compared to neonates may have contributed to higher levels of movement by juveniles between release and hibernation. These age-related differences in behavior should be incorporated into nursery-based management plans.**

Desert Tortoises (*Gopherus agassizii*) face serious population declines from a variety of causes, including disease, habitat loss, and predation. Hatcheries have been proposed as one mechanism for managing Desert Tortoise populations. Eggs laid in hatcheries would be protected from predation, and young tortoises could be similarly protected (Morafka et al., 1997). Older juveniles are larger and have more ossified shells and, therefore, may be more resistant to predation than neonates. However, behavior of young chelonians released from seminatural hatcheries could be affected by the length of time spent within the hatchery before release.

Previously, we examined differences in dispersal behavior between juvenile (8–9 years) and neonate (two months) Desert Tortoises (Hazard and Morafka, 2002). Recently released juvenile tortoises were more active than neonates and took longer to settle in a hibernation burrow. We hypothesized that juveniles were more active in part because they were more selective about their hibernation burrows and, therefore, had to move around more to find or excavate suitable burrows. Here, we examine differences in the characteristics of the hibernation burrows chosen by these tortoises, to evaluate potential selectivity by the two age classes.

Materials and Methods

We studied Desert Tortoises at the juvenile tortoise nursery at the U.S. Army National Training Center at Fort Irwin, California (Morafka et al., 1997). In October 1999, 12 neonates (hatched in the nursery within the previous two months) and 12 nursery-raised juvenile tortoises (8–9 years) were fitted with radiotransmitters (Holohil model BB2G, weighing 1.8 g), released near the pen, and periodically tracked (detailed methods in Hazard and Morafka, 2002). Tortoises ceased moving to new locations by day 34 (20 November 1999), and it was assumed that they were hibernating for the winter, though juvenile tortoises are facultative hibernators and may become active in winter if thermal conditions permit (Wilson et al., 1999a).

We located winter burrows for 22 tortoises (12 juvenile, 10 neonate) and marked them with pin flags in November 1999. We evaluated all burrows in February 2000, after the animals had emerged and

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Table 1. Characteristics of neonate and juvenile Desert Tortoises, their hibernation burrows, and two unoccupied burrows nearest to each occupied burrow. Means ± SD or (for burrow facing direction) angular deviation. Statistics for canopy cover are Chi-square values; all others are *F*-values.

					Effects					
	Occupied burrows		Unoccupied burrows		Age class		Burrow status		Age class × burrow status	
Variable	Neonate	Juvenile	Neonate	Juvenile	Statistic	*P*	Statistic	*P*	Statistic	*P*
Habitat										
Distance to nearest unoccupied burrow (cm)	114 ± 94	165 ± 140	—	—	0.942	0.343	—	—	—	—
Distance to 2nd nearest unoccupied burrow (cm)	176 ± 129	225 ± 172	—	—	0.558	0.464	—	—	—	—
Number of burrows with 0–50%/51–100% canopy cover	5/5	9/3	15/3	15/9	>0.0001	1.00	0.734	0.392	3.395	0.065
Distance to base of nearest shrub (cm)	52 ± 48	82 ± 78	67 ± 43	69 ± 61	1.143	0.289	0.006	0.938	0.939	0.336
Landscape slope (°)	2.6 ± 1.2	2.5 ± 0.5	4.3 ± 4.6	2.5 ± 0.4	2.056	0.157	1.687	0.199	1.687	0.199
Burrow slope (°)	8.3 ± 4.5	6.3 ± 3.8	8.6 ± 5.0	4.9 ± 2.5	7.263	0.009	0.240	0.626	0.600	0.442
Burrow size										
Tortoise width (mm)	38.6 ± 1.9	69.9 ± 6.1	—	—	209.6	<0.0001	—	—	—	—
Tortoise height (mm)	22.8 ± 1.1	38.6 ± 3.4	—	—	182.6	<0.0001	—	—	—	—
Burrow width (mm)	77.9 ± 17.2	114.9 ± 23.4	—	—	15.9	0.0008	—	—	—	—
Burrow height (mm)	42.0 ± 11.5	58.7 ± 8.8	—	—	14.2	0.0013	—	—	—	—
Burrow width: tortoise width	1.83 ± 0.78	1.68 ± 0.40	—	—	3.43	0.0797	—	—	—	—
Burrow height: tortoise height	1.84 ± 0.46	1.53 ± 0.30	—	—	3.39	0.0813	—	—	—	—
Burrow width × height: tortoise width × height	3.67 ± 1.3	2.60 ± 0.95	—	—	6.12	0.023	—	—	—	—
Burrow orientation										
Facing direction of burrow (°)	72.5 ± 73.8	162.3 ± 52.6	78.1 ± 67.1	111.7 ± 76.3	—	—	—	—	—	—
Rayleigh's test *z*-statistic and *P*-value	$z_{1,10} = 0.288$ $P > 0.50$	$z_{1,12} = 4.011$ $P = 0.015$	$z_{1,20} = 1.963$ $P > 0.10$	$z_{1,24} = 0.306$ $P > 0.50$	—	—	—	—	—	—

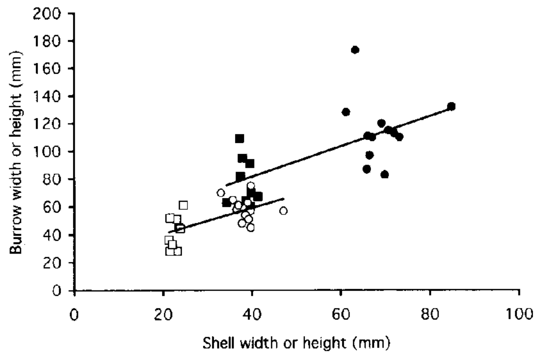

Fig. 1. Relationships between burrow size and Desert Tortoise size for neonate (squares) and juvenile (circles) Desert Tortoises. Burrow width (closed symbols) and height (open symbols) were significantly correlated with tortoise width and height when age classes were pooled. Width: y = 1.09x + 38.1; R^2 = 0.403; P = 0.002. Height: y = 0.925x + 22.1; R^2 = 0.368; P = 0.0035.

moved to new locations, to avoid disturbing them. We measured characteristics of the burrow chosen by the tortoise and of the two nearest unoccupied burrows that we judged (based on size) to be potentially usable by that animal. We recorded canopy species (if present), percentage canopy cover over the burrow, distance to the base of the nearest shrub, direction the mouth of the burrow faced, height and width of the burrow, slope of the ground immediately outside the burrow (burrow slope) and slope of the surrounding area (landscape slope). We also recorded distance from the two nearest unoccupied burrows to the tortoise's burrow. Compass bearings were corrected to true north. Data are presented as mean ± SD. Circular statistics were calculated according to Zar (1984); all other statistics were calculated using JMP (SAS Institute, Inc.). A P-value of 0.05 or less was considered significant.

Results

The dominant shrub species at the site were creosote (*Larrea tridentata*), box thorn (*Lycium pallidum*), and bur sage (*Ambrosia dumosa*); shrub species were pooled for statistical analysis. Percent canopy cover over burrows was bimodally distributed; therefore, burrows were categorized for analysis as having < 50% or > 50% cover. We found no significant differences between ages classes or between unoccupied and occupied burrows in canopy cover use, distance from burrow to the base of the nearest shrub, or overall landscape slope (Table 1). Burrow slope was typically steeper than landscape slope. Burrows associated with neonates (occupied or unoccupied) had a significantly steeper slope than those associated with juveniles; within age class, there were no differences between occupied or unoccupied burrows (Table 1). Appropriately sized alternative burrows (primarily rodent burrows) were typically found within 2 m of the hibernation burrow. There were no differences between age classes in distance to the nearest or second nearest unoccupied burrow (Table 1).

Juvenile tortoises were larger than neonate tortoises, and burrows used by juveniles were significantly larger

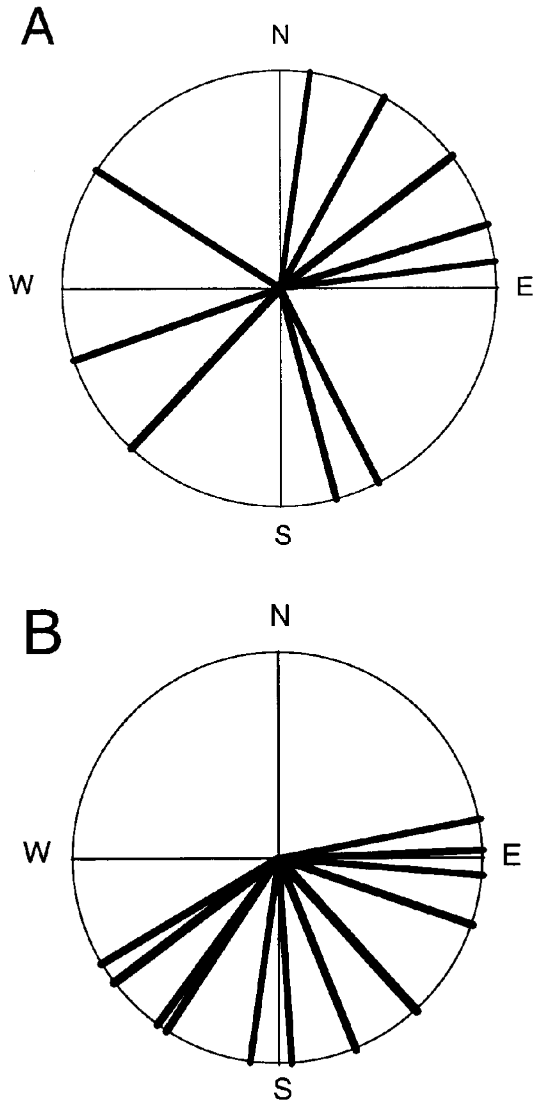

Fig. 2. Facing direction of hibernation burrows of (A) neonate (N = 10) and (B) juvenile (N = 12) Desert Tortoises. Compass directions corrected to true north (0°). Neonate mean vector direction was 72.5° but was not significantly different from random orientation (Rayleigh Test P = 0.975). Juvenile mean vector direction was 162.3 and was nonrandomly oriented (Rayleigh Test P = 0.015).

than neonate burrows (Table 1). Burrow height and width were both significantly correlated with tortoise size when age classes were pooled (Fig. 1). To evaluate fit of burrow size to tortoise size, we examined the ratios of burrow width to tortoise width, burrow height to tortoise height, and burrow "area" to tortoise "area" (width × height). Width ratio and height ratio did not differ between ages; however, relative area of the burrow mouth (burrow width × height/tortoise width × height) was significantly higher for neonates (Table 1). Unoccupied burrows were selected by us in part based on their size (roughly appropriate size for the individual tortoise); therefore, size of nearest neighbor burrows was not analyzed statistically.

Juvenile tortoises selected burrows that faced, on average, south-southeast (mean direction 162°), with a range of 79° to 233°; mean direction differed significantly from a uniform distribution ($P = 0.015$; Fig. 2B). Orientation of burrows used by neonate tortoises did not differ from a uniform distribution ($P = 0.975$; Fig. 2A). Available burrows did not appear to have a bias in their orientation; facing direction of the nearest unoccupied burrows for both neonates and juveniles did not differ from uniform distributions (Table 1).

Discussion

Juvenile tortoises do not appear to search farther for appropriately sized burrows than neonates do, because there was no difference between ages in distance to suitable unoccupied burrows. No differences in canopy cover, shrub species preference, or landscape slope were found, so juveniles do not appear to have selected burrows differently from neonates based on those criteria. Occupied and unoccupied neonate burrows had steeper slopes than did juvenile burrows, but this may be because the two age classes moved into slightly different habitats (Hazard and Morafka, 2002). Both juveniles and neonates made similar use of canopy cover: 80% of juveniles and 75% of neonates in this study had burrows within the canopy margin of a shrub. Juveniles confined in the pens were comparable; 80% of juvenile burrows within the natal pen were underneath the canopy (Wilson et al., 1999b).

The sizes of burrows used by juveniles were more similar to the sizes of the tortoises than were burrows used by neonates. Because juveniles often excavated preformed rodent burrows that may have been initially slightly smaller than the tortoise's cross-sectional dimensions, the burrows' height and width became similar to those of the occupying tortoise. In contrast, neonate Desert Tortoises frequently used existing rodent burrows that may have been substantially taller or wider than the tortoise and, thus, required little or no excavation.

Juvenile tortoises selected hibernation burrows that were nonrandomly oriented and faced, on average, south-southeast. The range was relatively narrow (79°–233°; Fig. 2). Juveniles kept within the pens used burrows with an average facing direction of 71° (east northeasterly) but a range that spanned the full compass (Wilson et al., 1999b). Burrows of juvenile tortoises at sites throughout the Mojave Desert tended to face westerly to southeasterly (Berry and Turner, 1986). Hibernacula of adult desert tortoises in the San Pedro River Valley in Arizona (Bailey et al., 1995) and the Whitewater Hills in California (Lovich and Daniels, 2000) were found primarily on south-facing slopes; burrow orientation itself was not measured in these studies.

Juvenile tortoises may have preferred burrows that faced the morning sun, allowing them to thermoregulate near the mouth of the burrow early in the day. Another possibility is that the burrows were selected because of their orientation relative to the slope of the landscape, as appears to be the case with *G. polyphemus* (McCoy et al., 1993). Direction of the local slope of each burrow was not measured in this study, but the overall landscape in the area used by the juveniles sloped downhill to the east. Regardless of the cause, the older tortoises exhibited a directional bias not seen in the neonates. If this bias caused juvenile tortoises to search longer for suitable burrows or burrow locations, it could explain the higher postrelease activity level of juvenile tortoises compared to neonates (Hazard and Morafka, 2002).

The increased activity level seen in juveniles could result in higher exposure to predation risk, possibly negating any benefits of larger size. Although no mortality was observed in either group during the 34 days between release and hibernation (Hazard and Morafka, 2002), sample size was relatively small.

Differences in burrow selectivity may reflect ontogenetic changes in dispersal behavior. Neonates may be predisposed to disperse as quickly as possible to a safe location in which to hibernate and wait out the dry autumn, emerging in the spring to forage and find a more permanent home. Not only is fall forage absent from the western Mojave Desert where summer monsoons are rare to nonexistent, but neonates function in the fall as postnatal lecithotrophs, surviving on the energetic and hydric reserves provided by or derived from residual yolk mass (Lance and Morafka, 2001). In contrast, eight- to nine-year-old juveniles who have been in the same location for years may not be prepared to disperse and when released in the fall may have been more focused on finding a suitable permanent burrow, not just a hibernaculum. Rather than dispersing when released, many of the juvenile tortoises in this study initially returned to the perimeter of the home pen (Hazard and Morafka, 2002), and some actually attempted to excavate under the predator-resistant hardware cloth barrier in an apparent attempt to return to their home burrows. These age-related differences in behavior need to be incorporated into future management plans involving long-term use of nurseries for conservation of desert tortoises.

Acknowledgments.—We thank S. Hillard and M. Marolda for assistance with mounting transmitters on tortoises; L. Bell, L. Cunningham, K. Emmerich, A. Johnson, M. Mendoza, B. Parker, and C. Todd for assistance with radio-tracking; and W. Alley for assistance with statistical analysis. Comments from two anonymous reviewers greatly improved the manuscript. Funding was awarded to the California State University, Dominguez Hills Foundation by the U.S. Army National Training Center, Fort Irwin California Directorate of Public Works, Department of Cultural and Natural Resources. Special thanks are extended to Department Manager M. Quillman for funding and support. This research was conducted under USFWS recovery permit CSUDH-5 issued to D. J. Morafka and a memorandum of understanding from the California Department of Fish and Game and was approved by the Chancellor's Animal Research Committee of the University of California, Los Angeles Office for the Protection of Research Subjects.

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Accepted: 24 May 2004.