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Comparative Dispersion of Neonate and Headstarted Juvenile Desert Tortoises (*Gopherus agassizii*): A Preliminary Assessment of Age Effects

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ABSTRACT. – Dispersal by young tortoises released from semi-natural hatcheries could be affected by the age of the tortoise or the length of time headstarted within the hatchery before release. Headstarted juveniles might be expected to remain closer to familiar territory than neonates. To test this, juvenile (6–8 yrs old) and neonate (< 2 mo old) desert tortoises (12 per group) were fitted with radiotransmitters and released from the hatchery at the Fort Irwin Study Site (National Training Center, Fort Irwin, California) in October 1999, and their movements tracked until all stopped moving (presumably hibernating) and no activity was observed, 34 days later. In the first 34 days after release, neonates generally moved to the northwest, uphill and away from the release point, while juveniles moved northeast, in the direction of their home hatchery 75 m away. Total distance traveled and final linear distance from the release site did not differ between age groups. Neonates moved less frequently and settled into hibernation locations more quickly than juveniles. There was no known mortality during the first 34 days post-release.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; dispersal; neonatology; headstart

Desert tortoises (*Gopherus agassizii*) are currently threatened by a number of factors, including disease-related mortality of adults and predation on juveniles by ravens and other human-subsidized predators (U.S. Fish and Wildlife Service, 1994). For these and other reasons, populations of tortoises are suffering alarming declines. Conservation of a long-lived species such as the desert tortoise may focus on increasing adult reproduction (in this case by reducing deaths due to disease), or by increasing juvenile survivorship. Reducing predation by protecting nests and then releasing neonates (individuals less than one year of age) may not be effective in long-lived chelonians if not coupled with protection of adults and older juveniles (here over one year old but not yet sexually mature; Morafka, 1994) (Congdon et al., 1994).

One mechanism for increasing juvenile survivorship is to protect them until they have grown large enough to be less susceptible to predators upon release (headstarting). A pilot study of the use of semi-natural enclosures for this purpose has been ongoing at the U.S. Army National Training Center, Fort Irwin, California, since 1989 (Morafka et al., 1997). Local female tortoises are brought to the enclosures from May to early July, allowed to deposit their eggs, and then returned to their site of capture. In 1999, young tortoises that had hatched in the enclosures ranged from 0–9 yrs old.

It is possible that long-term residence in such enclosures could affect the dispersal behavior and survivorship of juveniles when released. Older juveniles might be expected to remain closer to familiar territory than naive neonates, and the drive to disperse may be stronger at earlier ages. Alternatively, larger animals might be better able to travel further because of lower susceptibility to dehydration and other stresses, and due to longer strides. We examined dispersal by juvenile and neonate tortoises released from a long-term hatchery and holding area to determine whether age affected dispersal patterns.

METHODS

We studied dispersal at the juvenile tortoise nursery at the Fort Irwin Study Site (FISS), at the southeast corner of the U.S. Army National Training Center at Fort Irwin, California (35°06'N, 116°29'W; 650 m elevation). Predator-resistant enclosures were placed at the site in 1989, 1994, and 1998 (Morafka et al., 1997). Pens 1 and 2 are 60 m x 60 m fenced squares, while Pen 3 is a 20 m diameter circle about 75 m west of Pen 1; all have mesh roofs and subterranean hardware cloth walls to deter predators. Gravid female tortoises were collected from within an 8 km radius of the site in spring and early summer each year since 1991 and placed within the enclosures to lay their eggs. Females were returned to their capture sites within a month. When eggs hatched, some neonates were released and others retained in the pens for long-term studies. As a result, tortoises of varying ages were available for study.

In October 1999, we fitted 12 neonates (hatched within the previous 2 months) and 12 juvenile tortoises ranging in age from 8–9 yrs with radiotransmitters. All were released outside the pen, and their movements periodically tracked until March 2000. All of the juveniles and all but one neonate came from Pen 1; one neonate came from Pen 3. Half of each group was temporarily moved from Pen 1 to Pen 3 on 13 October prior to the 17 October release.

Transmitters (Holohil model BB2G) weighing 1.8 g were glued onto tortoise carapaces with Duro one-minute epoxy resin. Transmitters were fastened to the vertebral scute closest to the tail. The seams between neighboring scutes were protected from epoxy by first covering them with rubber cement, which was used because it is a flexible, non-durable substance that will degrade with prolonged environmental exposure.

We released tortoises on 17 October from Pen 3. Animals were equally distributed around the circumference of the pen (6–8 m apart), and one neonate and one juvenile were placed at each location, about 1–2 m apart. Using a Lotek STR1000 receiver, tortoises were located periodically for several months after release. We tracked tortoises in the fall on days 1, 3, 4, 7, 10, 13, 18, and 34 after release. 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 may become active in winter if thermal conditions permit (Wilson et al., 1999). Starting in February, animals were located on days 112, 127, 136, and 154 post-release. During this time, transmitters were removed from the juveniles, and transmitters on the neonates were replaced with ones with fresh batteries. Neonates were then tracked until June.

Each time a tortoise was located, data were collected as follows: time of observation, UTM coordinates and elevation of location (taken initially with a Garmin GPS III+, then in March with a high-accuracy Trimble GPS unit), compass direction from release point and from last known location, distance from release point and from last known location (measured with a meter wheel), microhabitat (perennial plant species present), location of the tortoise (e.g., under shrub, in burrow, in open), and whether the tortoise was directly observed.

Statistical Analysis. — To compare initial dispersal by juveniles and neonates, data from days 1, 7, and 34 post-release were used. Circular statistics (Rayleigh's test, Watson-Williams test) were calculated according to Zar (1984); all other statistics were done using SigmaStat 2.0 (Jandel Corporation). A p value of 0.05 or less was considered significant. When necessary, table-wide significance levels were evaluated using a sequential Bonferroni correction (Rice, 1989).

RESULTS

Direction of Dispersal. — Juvenile tortoises tended to move to the northeast, while neonates tended to move to the northwest (Table 1; Fig. 1). Because of high variance, angles were not significantly different from random distributions (Rayleigh's tests), but mean angles were significantly different between juveniles and neonates on all days (Watson-Williams tests). To test the hypothesis that tortoises were moving in the direction of their previous home, modified Rayleigh's tests were performed, comparing the mean angle for each day to 65°, the approximate direction of Pen 1 (the home pen) from Pen 3 (the release point), 75 m to the west. Angles for neonates were significantly different from 65° on all days. Mean angle for juveniles was not significantly different from 65° on all days, indicating that they were moving in the direction of Pen 1.

Distance Moved. — Linear distance from the release site on days 1, 7, and 34 varied widely within age groups (Table 2). We found no significant difference between age groups on any day, but did find a significant effect of day. Day 1 was significantly different from days 7 and 34, which did not differ from one another (Student-Newman-Keuls comparison); most movement occurred during the first week after release.

Total footpath distance traveled also varied widely within each age group. By day 34, neonates had traveled an average of 158 m, with a range of 44 to 432 m (Table 2). Similarly, juveniles had traveled a total of 66 to 385 m during that time. Again, there were no differences between age groups, but a significant effect of day. All three days differed significantly from one another (Student-Newman-Keuls comparison).

Elevation. — Elevation was used as an indicator of movement upslope or downslope. Repeated measures analysis of elevation showed a significant effect of age, no significant effect of day, and a significant interaction of age x day (Table 2). Neonates moved to higher eleva-

Table 1. Direction of dispersal by neonate and headstarted juvenile desert tortoises. Angular mean ± angular deviation (n). Orientation: z and p values for Rayleigh's test for uniform distribution. Comparison to 65°: u and p values for modified Rayleigh's test comparing mean angle to 65°, the direction of the home pen from the release site. Age effect: F and p for Watson-Williams tests comparing mean angles for neonates and juveniles within day; * = significance, with within-row sequential Bonferroni correction.

	Days post-release		
	1	7	34
Neonates			
Direction (°)	316 ± 55 (12)	307 ± 63 (11)	300 ± 61 (11)
Orientation (z, p)	3.409, 0.02	1.665, 0.20	2.120, 0.20
Comparison to 65° (u, p)	-0.863, >0.25	-0.849, >0.25	-1.19, >0.25
Juveniles			
Direction (°)	31 ± 54 (11)	51 ± 56 (12)	64 ± 52 (12)
Orientation (z, p)	3.388, 0.05	3.207, 0.05	4.248, 0.02
Comparison to 65° (u, p)	2.163, 0.025*	2.460, 0.01*	2.915, 0.0025*
Age Effect (F, p)	6.736, 0.025*	8.808, 0.01*	15.70, 0.001*

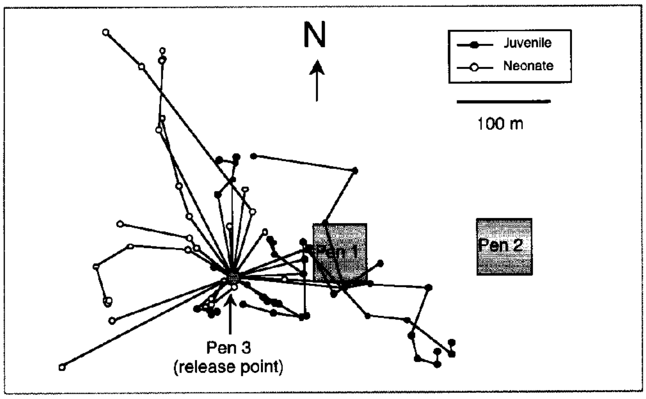

Figure 1. Movement of desert tortoises during first 34 days after release (one line for each animal). Pens 1, 2, and 3 indicated, with Pen 1 being the home pen for animals released at Pen 3. Tortoises whose paths appear to pass through Pen 1 actually moved around the perimeter of the pen.

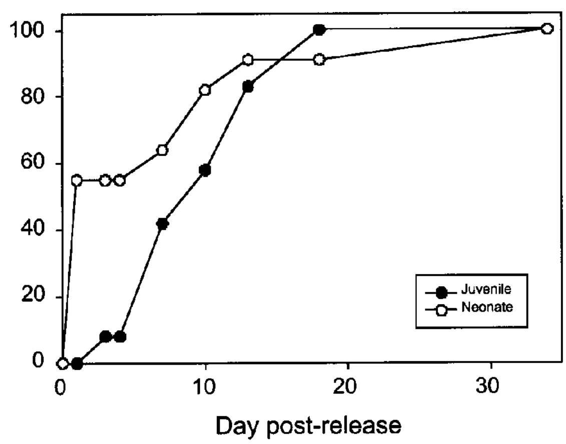

Figure 2. Percentage of juvenile (n = 12) and neonate (n = 11) desert tortoises located in the burrow in which they hibernated vs. days post-release.

tions than did juveniles; mean elevations did not differ significantly between age groups on day 1 (t = 1.438, p = 0.165), but did on day 7 (t = 2.65, p = 0.014) and day 34 (t = 3.129, p = 0.005).

Amount of Movement. — In the first 34 days (8 observations), juveniles moved more frequently than neonates, occupying 4.3 ± 1.2 locations per individual compared to 2.6 ± 2.2 for neonates (rank sum test T = 99.000, p = 0.045). Neonates established hibernation locations earlier in the first 34 days post-release (Fig. 2), and were seen out of burrows less frequently than juveniles (9.6 ± 15.0% of observations for neonates vs. 21.3 ± 9.8% for juveniles; t = 3.154, p = 0.0048).

Post-Hibernation Movement. — In the late winter (February and March), neonates were each located 4 times, and juveniles were located 3.33 ± 0.78 times. Animals were not all located the same number of times due to loss of battery power to some transmitters. During that time, neonates occupied 2.27 ± 0.90 locations per individual compared to 1.25 ± 0.45 for juveniles. Across the entire post-hibernation tracking period (February through August), neonates were located 7.64 ± 1.03 times and occupied 4.27 ± 1.49 locations per individual.

Apparent Survivorship. — All juveniles and 11 of 12 neonates survived until at least 1 March. One neonate lost its transmitter within a week of release, and its status could not be determined. Between 1 March and late August, one neonate and one juvenile were found dead, and two neonates lost their transmitters. The transmitters were recovered with signs of possible predation (tooth marks on one and loss of exterior coating of the other). The dead juvenile was found on 19 March upside-down about 4 m from its established burrow, and had a ca. 15 mm hole through the center of its plastron that appeared to have been caused by a predatory bird such as a raven. The dead neonate was found on 27 May partially buried in the soil; only a fragment of the carcass remained attached to the transmitter. Predation appeared to be the cause of death in both cases. Two neonates and two juveniles were observed to be alive in late August, but the status of the rest could not be determined. The carapace of one of the live juveniles had been recently damaged (puncture through the shell with soft tissue exposed), suggesting attempted predation, possibly by a raven.

DISCUSSION

Tortoises moved 10 to 250 m from their release point during the first month, then entered hibernation. The distances moved did not differ between age classes, but neonates tended to move uphill to the northwest, while juveniles

Table 2. Dispersal movements of neonate and headstarted juvenile desert tortoises. Mean ± s.d. Distance from release site is the straight-line distance from the location on that day to the outer edge of Pen 3, the release point. Total distance is the cumulative sum of the distances moved by an individual up to that time. Juvenile n = 12; neonate n = 12 on day 1 and 11 on days 7 and 34. F and p values for two-way repeated measures ANOVAS (age x day). Pairs of means in bold indicate a significant difference between neonates and juveniles (two-tailed t-tests with within-row sequential Bonferroni corrections); * = significance.

	Days post-release			Age effect		Day effect		Age x Day effect	
	1	7	34	F	p	F	p	F	p
Distance from release site (m)									
Neonates	82 ± 56	116 ± 91	126 ± 86	0.084	0.775	6.226	0.004*	0.393	0.677
Juveniles	83 ± 55	107 ± 76	108 ± 75						
Total distance traveled (m)									
Neonates	83 ± 57	144 ± 122	158 ± 116	1.625	0.216	19.330	<0.001*	1.373	0.264
Juveniles	96 ± 67	203 ± 102	219 ± 104						
Elevation (m)									
Neonates	685 ± 3.8	**686.5 ± 4.1**	**687.0 ± 4.0**	6.559	0.018*	0.125	0.883	4.232	0.021*
Juveniles	683.5 ± 3.8	**682.2 ± 3.4**	**682.2 ± 3.4**						

tended to move downhill to the northeast, in the direction of their natal pen. Juveniles were more active than neonates, occupying more locations per individual and taking longer to settle into a hibernation burrow. One possible reason for this is the larger size of the juveniles. Both groups appear to opportunistically use existing rodent burrows (and adult tortoise burrows, on occasion). Because of the small size of the neonates, they are able to use rodent burrows as initial shelters. Juveniles may have to search longer to find sufficiently large burrows or soil friable enough for them to construct their own burrow. In the late winter (February and March), neonates moved more often than juveniles, suggesting that perhaps once juveniles establish burrows they tend not to leave them, whereas neonates continue dispersing after hibernation. It is also possible that long-term captivity affected burrow usage by tortoises; captive-raised *Geochelone yniphora* in Madagascar made less use of vegetative cover after release in suitable habitat than did wild juveniles the same age (Pedrono and Sarovy, 2000).

There were no differences in mortality between neonates and juveniles from release until the transmitters were removed or replaced in March. Juveniles were not consistently tracked after this time, so we could not establish whether there were long-term differences in mortality. The transmitters lost by neonates in the spring could indicate mortality, but results were not conclusive. Spring tracking of both age classes would better address the issue of survivorship.

While there were no differences in the distances traveled by juveniles and neonates, the juveniles showed a tendency to move towards their old home, while neonates did not. However, other explanations are possible; perhaps older juveniles move downhill while neonates move uphill, for example. Further studies are needed to determine whether site fidelity influences juvenile movement, and whether it persists if animals are released from farther away. *Geochelone yniphora* of about the same age (8–9 yrs) showed no homing tendency when released a considerable distance from their hatching site (ca. 150 km; Pedrono and Sarovy, 2000). If juvenile site fidelity is significant, the implications for conservation need to be considered. Such behavior could have both positive and negative implications. If protected habitat for tortoises is limited, having the tortoises remain close to the hatchery could reduce the risk that they would move outside the boundaries of the protected area. However, such behavior would also increase the local population density, possibly increasing risk of disease transmission or predation.

It is clear that there are some differences in dispersal behavior between age classes, and these differences may affect conservation management of young tortoises. Further studies are needed to resolve these issues.

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