

POST-RELEASE DISPERSAL AND PREDATION OF HEAD-STARTED JUVENILE DESERT TORTOISES (*GOPHERUS AGASSIZII*): EFFECT OF RELEASE SITE DISTANCE ON HOMING BEHAVIOR

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Abstract.— Head-start nurseries have been proposed as a possible means of promoting recovery of Desert Tortoise populations. However, when released near their long-term nursery pens, juvenile Desert Tortoises (*Gopherus agassizii*) have been shown to initially attempt to return to their natal pen, which could have consequences for social interactions, spread of disease, and predation risk. We released 16 juvenile tortoises 500 m away from their home pen to determine whether this distance would eliminate such site fidelity. We tracked tortoises for three months following release. We monitored location, habitat use, activity, and survival. Tortoises showed no tendency to return to the natal pen following release; most settled into one location within two weeks of release. Seven of 16 tortoises were killed over a six-week period, apparently by a single Common Raven (*Corvus corax*). Predation risk was significantly affected by size; only tortoises with masses < 125 g were taken. Head-starting of tortoises to a larger size could result in higher survival rates, and releases at least 500 m from the natal pen could promote more normal dispersal. However, site fidelity could also be a useful management tool if it is desirable for tortoises to remain near their release location. Behaviors other than dispersal may also be altered by long-term residence in nursery pens, and further studies are warranted.

Key Words.— captive rearing; dispersal; head-start; homing; neonatology; predation; reintroduction

INTRODUCTION

Head-starting has been proposed as one means of promoting recovery of threatened Desert Tortoise (*Gopherus agassizii*) populations; older, larger juvenile tortoises are expected to be less vulnerable to predators such as coyotes and ravens upon release (USFWS 2008). However, long-term residence in nursery pens could result in changes to dispersal or other behaviors that could negate the benefits of larger size. We examined the influence of head-starting on juvenile tortoises using a long-term study site at the National Training Center, Fort Irwin, California, USA, which began head-starting studies in 1989

(Morafka et al. 1997).

In a previous study, we showed that when released within 70 m of their home pen in late fall, juvenile (8–9 yr old) tortoises behaved differently than neonates less than two months old (Hazard and Morafka 2002). Juveniles initially moved in the direction of their home pen, while neonates dispersed at random. Juveniles also spent more time active above ground before selecting a hibernation burrow, and were more selective about burrow characteristics, particularly the direction the burrow faced (Hazard and Morafka 2004). This homing tendency, increased activity, and burrow selectivity could result in higher predation rates if tortoises remain concentrated near the release

site rather than dispersing widely. We hypothesized that releasing juveniles further from their home pen would eliminate homing behavior, due to reduction of cues needed to orient toward the pen.

Here, we released tortoises that were raised in the same pen as in the previous study, but 500 m from the pen rather than 70 m. We then tracked movements to determine whether tortoises showed any bias in the direction of their movements, and we monitored activity and habitat usage. Incidental predation by a Common Raven (*Corvus corax*) at our site gave us an opportunity to evaluate predation risk.

MATERIALS AND METHODS

In 2001, we studied juvenile tortoise dispersal at the Fort Irwin Study Site (FISS) nursery, in the southeast corner of the U.S. Army National Training Center at Fort Irwin, California, USA (35°06'N, 116°29'W; 650 m elevation). Predator-resistant enclosures were established in 1989, 1994, and 1998 (Morafka et al. 1997). Pens 1 and 2 were 60 m x 60 m squares, Pen 3 was a 20 m diameter circle; all had mesh roofs to deter predators. Annually since 1991, gravid female tortoises were borrowed from adjacent habitat (8 km radius from FISS) in spring and early summer 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 immediately, while others were retained in the pens for long-term studies. As a result, tortoises of varying ages were available to address questions of dispersal and survivorship. Due to drought conditions, there was high neonate mortality in the enclosures during the winter of 2000–2001, and we had no neonates available for release in spring of 2001.

In March 2001, we fitted 16 juvenile tortoises ranging in age from 8–9 y with radio transmitters. We glued transmitters (Holohil model BD-2G) weighing 1.8 g onto tortoise carapaces with Duro One-minute Epoxy Resin. Transmitters were fas-

tened to the vertebral scute closest to the tail. We protected the seams between neighboring scutes 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 25 March. Using a compass and meter wheel, we placed groups of four animals approximately 500 m north, south, east and west of the natal pen (Pen I). We did not correct directions from magnetic to true north; we calculated actual distances from GPS coordinates to be 517 ± 8 (range 504–530) m from the pen. We released tortoises in late afternoon within about 10 m of each other in the shade of perennial shrubs (primarily Creosote, *Larrea tridentata*). Using a Lotek STR1000 receiver, we tracked and located tortoises on days 1, 2, 3, 7, 12–14, 20–21, 38–40, 54 and 91–92 after release. Tracking took place during daylight hours (between 0600 and 1900) but was not otherwise standardized to a particular time of day. We removed transmitters on day 91 or 92 from surviving tortoises, which were left in the wild. We did not collect detailed data at that time and we used only data from days 1–54 for analysis.

Each time a tortoise was located, we recorded time of observation, Universal Transverse Mercator (UTM) coordinates of the location (Garmin GPS III+, accurate to within 4.7 ± 0.8 m), compass direction and distance (measured with a meter wheel) from the release point and from the last known location, microhabitat (perennial plant species immediately above or adjacent to the tortoise) and location of the tortoise (e.g., under shrub, in burrow, in open). We calculated distance from the natal pen to each location from the UTM coordinates and total path distance traveled by a tortoise by summing the distances between sequential observed locations, giving a cumulative serial linear distance.

We measured tortoise mass, carapace length, carapace width, and shell height prior to release and again when transmitters were removed (for surviving animals), and we used these values

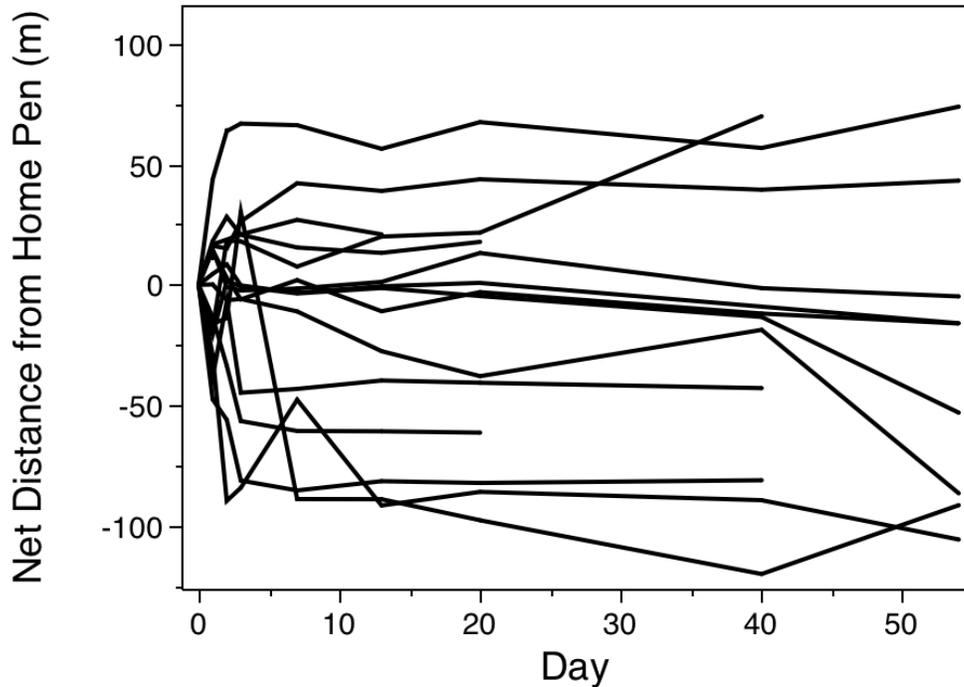


FIGURE 1. Distance from the natal pen for the first 54 days following release of juvenile Desert Tortoises (*Gopherus agassizii*) from their natal pen. Distance is standardized to the initial distance from the pen for each individual at the time of release (range 504–530 m). Each solid line represents an individual tortoise; one outlier (see text) was left out for clarity. Lines that end before day 54 indicate animals that were killed by a Common Raven (*Corvus corax*).

to calculate a condition index for each tortoise, which is a measure of tortoise hydration and physical condition. We calculated condition index as $\text{mass}/(\text{carapace length} \times \text{carapace width} \times \text{shell height})$ in g/cm^3 , and compared this to a standard value of $0.64 \text{ g}/\text{cm}^3$ for tortoises in prime condition (Nagy et al. 2002). We present data as a percentage of that standard value (% prime). We made statistical analyses using JMP 8.0 for Max OS X, with $P \leq 0.05$ considered significant.

If an animal moved in an irregular pattern that nevertheless took it in the general direction of the pen over time, analysis of direction of movement for any particular day might not truly indicate that the tortoise was moving toward the pen. We therefore decided to focus our analysis on a simpler measure: change in the distance from the

natal pen after release, standardized to the initial release distance for each tortoise. One individual from the northern release site moved substantially further than the others (path distance over 1600 m). Therefore we made statistical analyses using all animals and also with this individual excluded. Hereafter if exclusion of this outlier changed the conclusions, we presented both sets of results.

Most tortoise dispersal from the release site occurred in the first few days of release; after that, most animals remained in one location or moved only small distances (Fig. 1). We tested for homing tendencies in two ways. First, for each observation day, we compared the mean net distance from the pen relative to the release point of each individual to a mean of zero (the mean expected if there was no movement, on

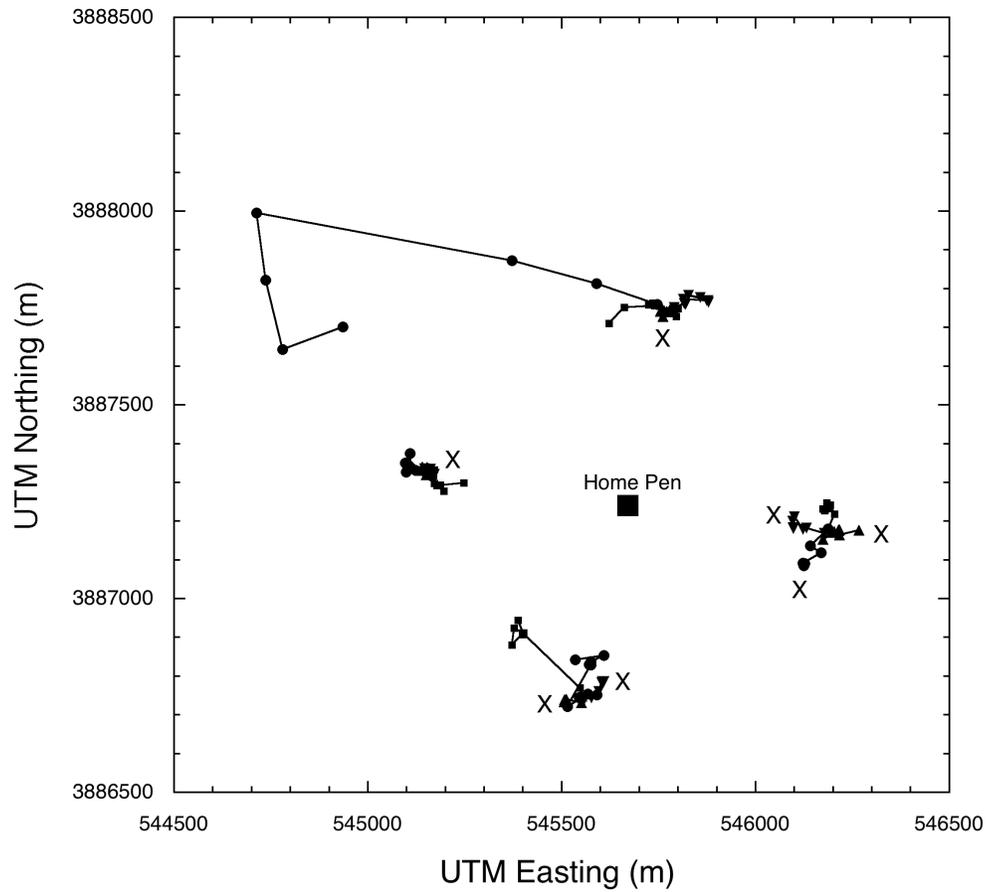


FIGURE 2. Movements by juvenile Desert Tortoises (*Gopherus agassizii*) relocated 500 m north, south, east, or west of their natal pen. Coordinates are UTM easting and northing locations within UTM Zone 11S. Each line represents movement of an individual animal. “X” denotes tortoises that were predated by a Common Raven (*Corvus corax*).

average, toward the pen). Second, we tested for a relationship between time (Day) and net distance in a factorial ANOVA using Day, tortoise ID (as a random effect for repeated measures), and their interaction as effects in the model, to evaluate whether there was a tendency to move closer over time.

RESULTS

Movement and homing behavior.—Following release, tortoises moved varying distances from their release sites (Fig. 2). Most tortoises stayed within about 100 m of their release site; mean distance from the release points on day 54 post-release was 174 ± 249.7 m, (98.8 ± 78.7 m with the outlier removed; Table 1). On each observation day the mean net movement toward the pen never differed from zero (Table 1). In a factorial test for a time effect on distance, results differed depending on the inclusion of the outlier animal. With all animals included, the overall model r^2 was 0.656; tortoise ID explained 58% of the variance. There was no significant effect of Day ($P = 0.934$) or day x ID interaction ($P = 0.242$). When the outlier was removed, the overall model r^2 was 0.837 and tortoise ID explained 77.6% of the variance. There were significant effects of both day ($P = 0.015$) and day x ID interaction ($P < 0.001$). However, the magnitude of the effect of day was relatively small, with an estimated slope of -0.44 ± 0.18 m/day. Overall, different tortoises moved considerably different distances, and while there was a slight tendency to move closer to the pens with time, the magnitude of the distance moved was small. With the exception of the outlier, no individual moved far enough, overall, to cover the distance back to the pen. Even the individual that moved closest to the pen only covered 100 m of the 500 m between the release point and the pen.

Habitat use and activity.—Of 134 observations, we located tortoises within burrows for

48% of all observations (39% in burrows under canopy, and 9% in burrows in the open), out of burrows in the shade for 38% of observations, and out of burrows in the open for 14% of observations. The main shrubs used as cover were Creosote (33% of observations), Bur Sage (*Ambrosia dumosa*, 27%), and Box Thorn (*Lycium pallidum*, 12%). Smaller perennials were used as cover less frequently, with Ephedra (*Ephedra* sp.), Big Galleta (*Hilaria rigida*), and Littleleaf Ratany (*Krameria erecta*) together comprising the remaining 10% of observations. Note that these observations are not truly independent and include multiple observations of the same tortoise in the same location, and we did not adjust for time of day or for date, which influenced activity. Tortoises were more likely to be found out of burrows early in the study, with a significant interaction between day and time of day (nominal logistic regression: effect of day $P < 0.001$, effect of time of day $P = 0.117$, effect of day \times time of day $P = 0.005$).

Movement.—By day 13 post-release, 13 of 16 tortoises had settled into “permanent” locations and did not move substantially for the remainder of the study. The remaining three individuals moved to new locations continuously. Animals moved a total path distance of 255 m on average (Table 2; the mean dropped to 163 m when one outlier who travelled > 1600 m was excluded). Animals on average occupied 6.5 independent locations during the three month observation (in which they were located nine times), and were seen out of their burrows and active 48% of the time (Table 2).

Predation.—Between day 21 and day 64, seven transmittered tortoises were killed, apparently by a single Common Raven. We found their carcasses with transmitters still functional around the base of a group of powerline pylons approximately 3 km from the site. We also found five dead wild juveniles during this time: one near Pen 2, and four in the vicinity of the dead trans-

TABLE 1. Dispersal by juvenile Desert Tortoises (*Gopherus agassizii*) following release. Net distance from the home pen was standardized to the initial distance from the pen for each individual at the time of release, mean \pm S.D. The t-tests test each day's mean against a predicted mean value of zero (no net movement toward the pen). Distance from the release point (mean \pm s) is given both with the outlier individual included (upper values) and with it excluded (lower values). Data for the outlier were not available on day 40.

Days Post-release	n	Net distance from home pen (m)	t; P	Distance from release point (m)	Distance from release point (m) outliers removed
1	16	-2.72 \pm 24.5	-0.4454; 0.6624	31.1 \pm 16.6	30.2 \pm 16.8
2	16	0.88 \pm 38.7	0.0919; 0.9280	62.3 \pm 65.1	52.5 \pm 53.8
3	16	5.42 \pm 63.2	0.3429; 0.7364	84.5 \pm 111.1	61.1 \pm 62.1
7	16	32.5 \pm 184.6	0.7059; 0.4911	133.6 \pm 264.2	68.9 \pm 55.1
13	16	20.9 \pm 157.4	0.5322; 0.6024	129.0 \pm 252.1	67.3 \pm 53.6
20	15	14.4 <i>pm</i> 133.5	0.4170; 0.6830	134.2 \pm 248.3	71.5 \pm 54.4
40	11	-19.3 \pm 60.7	-1.0520; 0.3175	n/a	81.6 \pm 61.5
54	10	9.85 \pm 134.1	0.2321; 0.8217	174.3 \pm 249.7	98.8 \pm 78.7

mitted tortoises near the powerline pylons. All appeared to have been killed relatively recently and were similar in size to the transmitted tortoises, though due to their condition, we could not determine precise sizes. We saw a single raven at the site and on the powerline pylons during this time, and we believe it to have been responsible for the predation; no other avian tortoise predators were observed.

Size and condition had significant effects on survival. All seven of the tortoises that were predated had initial masses of 125 g or lower and carapace length of 84 mm or lower; all but one of the nine tortoises who survived was > 125 g

and all but two had carapace lengths of 84 mm or longer (Fig. 3). Predated and surviving tortoises differed significantly in initial mass and carapace length, but not initial condition index (Table 3). Differences in activity level appeared to have no effect on predation risk; predated and surviving tortoises did not differ in how frequently they were observed out of their burrows or the number of different sites they occupied (Table 3).

DISCUSSION

Tortoise movement.—Post-release, 81% of tortoises settled within a few days into new locations

TABLE 2. Post-release movement (m) by head-started juvenile Desert Tortoises (*Gopherus agassizii*) showing means \pm s (range). Within a line, means sharing a superscript did not differ significantly (ANOVA and Tukey's post-tests). Analysis for total path distance was done both with and without the outlier point.

	Spring 2001 Release Juveniles (n = 16) ¹	Fall 1999 Release Juveniles (n = 12) ²	Fall 1999 Release Neonates (n = 11) ²
Number of observations	9	8	8
Total path distance travelled (m) ³	255 \pm 383 (42-1637) ^{4, a} 163 \pm 108 (42-391) ^{5, a}	219 \pm 104 (66-385) ^a	158 \pm 116 (44-131) ^a
Number of different locations occupied	6.9 \pm 1.9 (4-10) ^a	4.3 \pm 1.2 (2-6) ^b	2.6 \pm 2.2 (1-7) ^c
Percent of observations in which tortoises were observed out of burrows	48.6 \pm 17.6 (14.3-70) ^a	21.3 \pm 9.8 (12.5-62.5) ^b	9.6 \pm 15 (0-37.5) ^b

within 100 m of their release site, and then moved relatively little. The average distance moved by tortoises from their release points was similar regardless of distance from the pen: juveniles released 70 m from the pen moved 108 ± 75 m from their release points by 34 days post-release (Hazard and Morafka 2002). This suggests that, at least in the short term, juvenile tortoises will generally stay relatively close to their release point (although there is clearly substantial variation among individuals). This is in contrast to adult desert tortoises, which when relocated may move several kilometers (Berry 1986); the reasons for this apparent ontogenetic change are unclear.

Juvenile tortoises did not appear to show homing behavior when released 500 m from their home pen, in contrast to the prior release closer to the pen (Hazard and Morafka 2002). It is possible that this distance resulted from a lack of cues, such as visual, spatial, or olfactory

cues, necessary to help them navigate back to familiar territory. Head-started Ploughshare Tortoises (*Geochelone yniphora*) of roughly the same age also did not show homing behavior when released over > 150 km from their natal pens (Pedrono and Sarovy 2000), but instead remained close to their release site following a “soft” release (four weeks of acclimation in pens at the release site prior to release).

Habitat use and activity.—Tortoises primarily took shelter and dug burrows near the dominant shrubs in the area (Creosote, Bur Sage, and Box Thorn), but because habitat selection was not a focus of this study, we did not quantify abundances of the shrub species in the area to determine whether tortoises showed preference for certain shrub species. Juvenile desert tortoises released in the spring (current study) showed higher activity level than either juveniles or

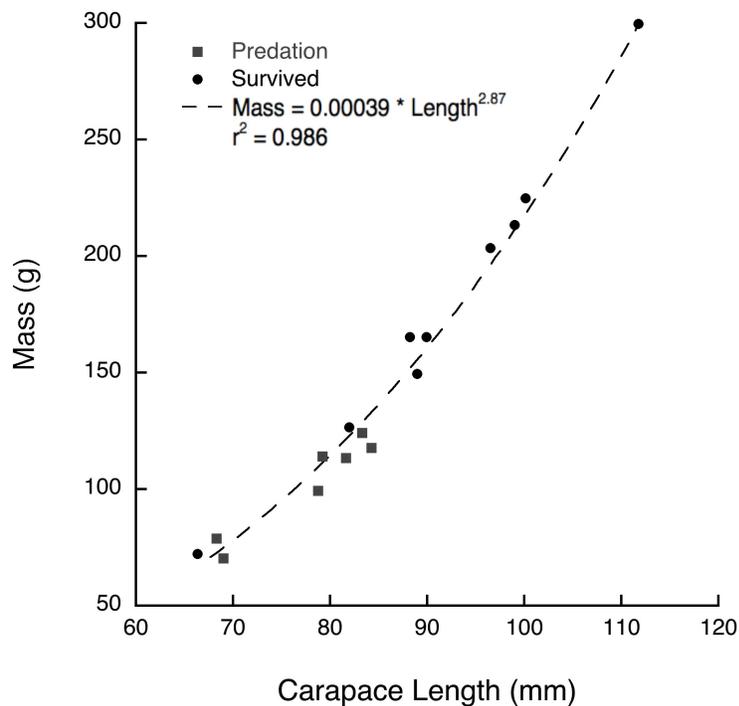


FIGURE 3. Body mass (g) vs. carapace length (mm) of juvenile Desert Tortoises (*Gopherus agassizii*) that were (squares) or were not (circles) killed by a Common Raven (*Corvus corax*).

neonates released in the fall prior to hibernation (Hazard and Morafka 2002). Distance travelled during the tracking period did not differ among the groups, but tortoises in the current study were found in a higher number of different locations during the observation period, and were observed out of their burrows much more frequently. Activity level did not affect risk of predation in the spring release. The lower activity in the fall could potentially have contributed to the lack of observed predation (Hazard and Morafka 2002).

Predation.—Ravens are effective predators of juvenile Desert Tortoises (Boarman 2003). The predation events we documented appeared to have been caused by a single raven that came to our site, feasted on the smaller juvenile tortoises for a few weeks, and then moved on to

another location, possibly because availability of vulnerable tortoises decreased. We had used flagging tape on shrubs to mark tortoise burrows, and it is possible that this facilitated foraging by the raven; once predation began, we removed all of the flagging.

Our observations allow us to make some estimates of possible predation rates by ravens, and the nutritional implications for the raven. If our assumption that a single raven was responsible is correct, then one raven killed seven transmitters and five wild tortoises in six weeks, leading to an overall predation rate of two tortoises per week, or 0.28 tortoises per day. The field metabolic rate (FMR) of ravens can be estimated based on existing equations for FMR estimates for passerines (Nagy et al. 1999), where FMR in kJ/d equals $10.4(\text{mass in g})^{0.68}$. A 1,200 g raven (estimated

TABLE 3. Factors influencing juvenile Desert Tortoises (*Gopherus agassizii*) predation risk showing means \pm s and range for traits. Number of locations occupied was restricted to the first six observations (prior to onset of predation) to avoid bias due to fewer observations on predated tortoises.

Trait	No (n = 9)	Yes (n = 7)	<i>t</i> ; <i>P</i>
Mass (g)	180 \pm 65.0 (72.2-299.7)	102.6 \pm 20.7 (70.4-124.2)	3.36; 0.0072*
Carapace length (mm)	91.4 \pm 12.8 (66.3-111.8)	77.8 \pm 6.5 (66.3-84.3)	2.76; 0.0167
Condition index value (% of prime)	96.5 \pm 3.8 (91.7-101.7)	92.2 \pm 4.9 (85.9-101.0)	1.909; 0.0821
Percent of observations in which tortoises were observed out of burrows	51.9 \pm 16.7 (33.3-77.8)	44.3 \pm 19.2 (16.7-66.7)	0.819; 0.4284
Number of different locations occupied	6.00 \pm 1.32 (4-8)	4.85 \pm 0.90 (4-6)	2.052; 0.0596

average body mass for Common Ravens, Dunning 1993) would therefore have an estimated FMR of 1291 kJ/d. Using an estimated metabolizable energy content of 16.1 kJ/g dry matter for vertebrates eaten by birds (Nagy et al. 1999), a raven would need to consume approximately 80 g of dry matter per day. Juvenile tortoises are approximately 25% dry matter by mass (Nagy et al. 1997); however, much of this mass is shell, and ravens generally do not consume the entire tortoise. In our study, we made no attempt to quantify the amount of tortoise tissue consumed. As a very rough estimate, if we assume that a raven took the largest tortoises possible (125 g) and that it ate half of each tortoise, it would gain approximately 15 g of dry matter per tortoise. At an average of 0.28 tortoises per day, the raven would obtain just over 4 g of dry matter per day

from tortoises, or about 5% of its daily requirement.

The raven involved in predation in this study appeared to have a slightly lower maximum size threshold for tortoise prey than has been previously reported. Several prior studies (reviewed in Boarman 2003) found a maximum carapace length of 100 mm, compared to the maximum of 84 mm in this study. Our raven seemed to feed on top of powerline pylons, and was therefore limited to animals it was capable of carrying (those below 125 g or 84 mm). Other ravens may eat tortoises where they find them, and would be capable of taking larger juveniles. However, tortoise carcasses as great as 100 mm carapace length have been found below raven nests (Boarman 2003), demonstrating that other ravens can carry larger prey, so perhaps this individual raven

was less able or willing to take larger prey than others.

The previous tortoise release at this site found no mortality during the month between release and hibernation; while animals were not systematically tracked when they emerged in the spring, there were some observations of apparent predation then (Hazard and Morafka 2002). It is possible that there are seasonal differences in predation risk, and that animals are less at risk during the fall. However, there is insufficient data at this time to draw any such conclusions.

Implications for head-starting.—Head-starting of tortoises to a larger size could substantially reduce vulnerability to predators, resulting in higher survival rates. While this would mean keeping animals in captivity or semi-captivity for longer, the impact on predation risk appears to be dramatic. In this particular case, 100% of the animals over 125 g avoided raven predation, while 87.5% (seven of eight) below that threshold were taken. Management techniques aimed at increasing growth rate (for example, supplementing food or water in semi-natural pens) could reduce the time in captivity prior to release.

Juvenile tortoises released within 70 m of their home pen showed strong site fidelity (Hazard and Morafka 2002), but in the present study, tortoises released 500 m from the pen did not show such tendencies. Depending on particular management requirements, managers could view site fidelity by juvenile tortoises either positively or negatively. Overcrowding of head-started tortoises near their home pen due to site fidelity could increase density-dependent predation risk or disease transmission, or affect social interactions. Release of juveniles 500 m from the natal pen could promote normal dispersal, reducing homing behavior and crowding. On the other hand, if it is desirable to minimize dispersal by animals (for example, if available suitable or protected habitat is relatively small), promoting site fidelity could be used as a tool to encourage this

behavior.

Behaviors other than dispersal may also be altered by long-term residence in nursery pens (Alberts 2007). While we found no obvious differences in habitat use, social or foraging behaviors could potentially be affected. For example, tortoises raised in close proximity may interact differently with conspecifics in the wild. Also, diversity of potential food plants within the pen could influence ability or willingness to forage on novel foods outside the pen (however, see Oftedal 2002 on how tortoise select plants to eat). Further studies of the influence of long-term head-starting on these and other aspects of juvenile tortoise biology are warranted.

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emerging diseases in New Jersey amphibians. She earned a BS in Biology (Ecology, Systematics and Evolution concentration) from Cornell University and a PhD in Physiology from the University of California, Riverside. Her postdoctoral research at UCLA on juvenile desert tortoise biology was completed under the mentorship of Ken Nagy and Dave Morafka; she completed additional postdoctoral work at the University of California, Santa Cruz. She is currently on the Board of Governors of the Society for the Study of Amphibians and Reptiles. (Photographed with Diamond-Backed Terrapin by Paola Dolcemascolo).



DAVID J. MORAFKA was a key contributor to the literature on the herpetofauna of the southwestern United States, and particularly the Mojave Desert. He received his bachelor's degree in Zoology from the University of California at Berkeley, and his doctorate in Biology from the University of Southern California. He spent thirty years on the faculty at California State University, Dominguez Hills, until his retirement in 2002, and at the time of his death in 2004 was a Research Associate at the California Academy of Sciences in San Francisco. One of his major contributions to the field was his wide-ranging collaborative work on the neonatology of Desert Tortoises, facilitated by his relationship with the US Army National Training Center at Fort Irwin, California, where he established a research facility for the study of young tortoises in semi-natural enclosures. He

will be remembered especially for his generosity and his unfailing support of student researchers, whom he treated as junior colleagues, and for his efforts toward reptile conservation in the arid Southwest. (Photographed, with his wife Sylvia Papadakos-Morafka, by Lisa Hazard).



SCOTT HILLARD is a Research Scientist in the Department of Ecology and Evolutionary Biology at UCLA. Scott received his Bachelor's degree in Biology from the University of Kansas in 1989. For his graduate work at Colorado State University (1996), he studied the biophysical ecology of juvenile Desert Tortoises (*Gopherus agassizii*). After earning his Master's degree, Scott studied with the father of tortoise head-starting, Dr. David Morafka. He has continued pursuing questions in tortoise ecology and biology, and with techniques in tortoise head-starting (following the egg until it becomes a reproductive adult) through today. He has worked closely with Dr. Ken Nagy since 2003 on tortoise head-starting research on military bases in the California Mojave Desert. Since 2006, Scott has also served as an advisor, and since 2010 as both advisor and the 'man on the ground', for the highly successful Bolson Tortoise (*Gopherus flavomarginatus*) head-starting and restoration program sponsored by the Turner Endangered Species Fund on two of Ted Turner's ranches in New Mexico. (Pho-

Hazard et al.—2010 Head-starting Symposium: Effect of release site distance on homing.

tographed with Bolson Tortoise by Myles Traphagen).