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HEAD-STARTED DESERT TORTOISES (*GOPHERUS AGASSIZII*): MOVEMENTS, SURVIVORSHIP AND MORTALITY CAUSES FOLLOWING THEIR RELEASE

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Abstract.—We released and monitored 53 juvenile Agassiz's Desert Tortoises (*Gopherus agassizii*), aged two to 15 y, that were hatched and head-started inside predator-resistant field enclosures. We set free these tortoises under a variety of conditions to evaluate effects of release distance, season of release, and age/body size on homing behavior and survivorship. Some juveniles moved large distances following release, but homing itself was undetectable. The lack of homing behaviors was likely due to release distance and selection of release sites out of the line-of-sight of natal enclosures. The use of small halfway-house enclosures to accustom some relocated juveniles to release sites for four months before release (i.e. “soft release”) had no effect on subsequent movements or survivorship during the first year following release. Survivorship was not affected by distance of release from natal enclosures, which ranged from 546 m to 1.4 km. Survivorship through one year was similar for juveniles released in spring or autumn. After two years, most small juveniles had been killed by predators, but survivorship increased with body size and age. Juveniles over approximately 100 mm MCL (midline carapace length) and nine years of age when released exhibited high survivorship. However, following a long drought the previous two years, predation by Coyotes (*Canis latrans*) was heavy on these larger juveniles in the third year after release. Thus, survivorship after three years was relatively low (34%) with the youngest, smallest cohort (two years old when released) exhibiting the lowest survivorship (4%). We recommend releasing head-started tortoises after they attain a body size of larger than 100 mm MCL and selecting release sites at least 546 m from enclosures.

Key Words.—Agassiz's Desert Tortoise; conservation; growth; head-start; homing; predation

INTRODUCTION

The Agassiz's Desert Tortoise (*Gopherus agassizii*, Murphy et al. 2011), which inhabits the Mojave and Colorado deserts in California, Nevada, Utah and Arizona, was listed as a Threatened Species in 1990 following major declines in population densities in the western part of the species range (United States Fish and Wildlife Service [USFWS] 1990). Desert Tortoises are herbivorous reptiles characterized by high survivorship of long-lived adults (Turner et al. 1984), low female fecundity (Turner et al. 1986; Mueller et al. 1998; Wallis et al. 1999), low survivorship of eggs and juveniles (Bjurlin and Bissonette 2004), and slow growth and delayed maturity (Turner et al. 1987). These life-history characteristics make tortoise populations particularly vulnerable to a wide range of natural and anthropogenic threats.

Scientists, wildlife managers, and conservationists have applied a variety of techniques to protect, conserve, and recover declining turtle and tortoise populations.

For example, one method is head-starting, which has a long history as a popular conservation procedure for marine turtles (Huff 1989). Head-starting is a technique whereby juvenile turtles or tortoises are hatched and raised in predator-resistant field enclosures for later release. This procedure has been quite successful in restoring Galapagos tortoise (*Chelonoidis* spp.) populations on Pinzón Island (Caporaso 1991). The main purpose of head-starting is to reduce the large losses of vulnerable eggs and young tortoises to predators (Morafka 1994; Heppell et al. 1996; Morafka et al. 1997). An additional goal for head-starting Agassiz's Desert Tortoises is to reduce juvenile mortality from drought and starvation during years of low rainfall (Nagy et al. 1997, in press). Head-starting has been criticized as a recovery technique for populations of tortoises because it is slow, costly, and difficult to validate (Crouse et al. 1987; Reed et al. 2009; Fish and Wildlife Service 2011).

Despite these cautions, head-starting efforts are currently being implemented to help recover Desert Tortoise populations and those of many other chelonian

species. Though the purpose of this investigation was not to evaluate the long-term value of the technique, we believe it may be useful if applied selectively and in conjunction with other conservation measures. We argue below that head-starting Mojave Desert Tortoises may be one of only a few recovery tools likely to be successful in the western part of their range.

We conducted this study to evaluate different protocols for releasing head-started Agassiz's Desert Tortoises back into the wild. We had the opportunity to release and monitor the success of over 50 head-started juveniles of various ages and sizes from a hatchery-nursery located in natural habitat in the Western Mojave Recovery Unit (USFWS 2011), and we evaluated release parameters thought to be important in determining successful release events. Several testable hypotheses emerged from consideration of the following points. In an earlier study at the same hatchery-nursery, older head-started juvenile tortoises attempted to return back to the nursery after release near the enclosures, whereas released neonates tended to disperse (Hazard and Morafka 2002). Homing tortoises on the move may risk overheating and are probably more vulnerable to detection by predators. Also, predation may be higher on juvenile tortoises released in spring, when several species of predators (mainly ravens and hawks) are raising their own young, than in autumn. Mortality can be relatively high among very young tortoises (Bjurlin and Bissonette 2004), but survivorship increases with body size (Averill-Murray 2002). Thus, we designed experiments to test the hypotheses that: (1) more of the older, larger juveniles would attempt to go home to the hatchery/nursery enclosures shortly after release than would smaller juveniles; (2) keeping juveniles inside halfway houses at the release sites until they settled into burrows would reduce homing attempts upon their later release; (3) juveniles released farther from home would be less likely to try to go home than would those released closer to the head-start enclosures; (4) juveniles released in autumn would experience higher survivorship than those released in spring; and (5) older, larger released juveniles would have higher survivorship than younger, smaller juveniles.

MATERIALS AND METHODS

Study site and animals.—We studied Agassiz's Desert Tortoise juveniles in their natural habitat from September 2005 to December 2008 at the Fort Irwin Study Site (FISS; 35°08' N, 116°30' W) in the southeast corner of the Fort Irwin National Training Center (U. S. Army), about 58 km northeast of Barstow, San Bernardino County, California. The vegetation at this central Mojave Desert site is comprised of a typical Creosote Bush (*Larrea tridentata*) and Burro-weed (*Ambrosia dumosa*) plant association. We obtained

monthly rainfall totals from the Brinkman 3 weather station at Fort Irwin, California, approximately 27 km (17 mi) WNW of our study site. This was the closest weather station that had complete rainfall records for the full study period.

The site included three fenced and netted predator-resistant enclosures containing natural vegetation that have served as tortoise hatchery-nursery facilities for head-start studies since 1990. We captured gravid wild females locally, and placed them in one of these three enclosures where they eventually dug nests and deposited eggs. Following egg laying, we returned the females to their capture sites and released them into a burrow. The nests, eggs, and resulting head-started hatchlings have been involved in a variety of studies (Nagy et al. 1997; Wilson et al. 1999a, b; Oftedal et al. 2002; Baxter et al. 2008). The enclosures received only natural rainfall (no supplemental irrigation), and no additional food was provided to resident tortoises.

In 2005, there were many juveniles still living in the enclosures, ranging in age from two to 15 y. We used 53 of these to study the success of various release procedures. These juveniles represented seven age cohorts in autumn 2005: 2 y-olds (2003 cohort, $n = 23$), an 8 y-old, 9 y-olds ($n = 2$), a 10 y-old, 13 y-olds ($n = 4$), 14 y-olds ($n = 15$), and 15 y-olds ($n = 7$). Subsequently, for analysis purposes, we also sorted juveniles into four size groups for examining growth rates and size-related causes of mortality: initial midline carapace length (MCL) of 45–80 mm (all 2 y-olds when released), MCL 81–110 mm (mixed eight to 15 y-olds when released), 111–140 mm (all 14–15 y-olds when released), and 141–175 mm (all 14–15 y-olds when released). We also sorted juveniles into eight smaller size groups (see details below) to achieve better resolution for analyzing survivorship curves.

Numbering and attaching transmitters.—We assigned all tortoises unique numbers for identification (ID). These IDs were written on both their carapaces and plastrons with indelible ink and were also applied more permanently by using clear epoxy glue to affix a paper ID tag into a recessed region of a carapacial scute. Following Boarman et al. (1998), we also fitted each tortoise with a Holohil model BD-2, PD-2, or RI-2B radio-transmitter appropriately selected for the tortoises' body sizes at the time of release (Holohil Systems Ltd., Carp, Ontario, Canada). We ensured that transmitter packages weighed no more than 5% of the initial body mass of a tortoise, as specified in our USFWS permit.

Release and monitoring methods.—We released tortoises head-first into appropriately-sized burrows that we excavated for them or that were already present (e.g., vacated rodent burrows) after we cleaned them of debris and cobwebs. We monitored tortoise behavior

immediately after release and over the next several days. We placed tortoises that did not accept the first burrow they were offered in nearby burrows that we prepared. Within a day or two, all released tortoises settled into a burrow of some kind.

Using Lotek STR 1000 receivers (Lotek Wireless Inc., Newmarket, Ontario, Canada) and Telonics RA-2AK Yagi antennas (Telonics, Inc., Mesa, Arizona, USA), we radio-tracked tortoises bi-weekly from spring through early summer (March–July), then monthly during low activity periods (August–February). During high activity or high predation periods, we tracked tortoises more frequently, usually at least weekly. For each telemetry relocation, we recorded whether a tortoise was invisible underground, underground but visible in the burrow, or above ground, and its Universal Transverse Mercator (UTM) coordinates, using Garmin GPSMAP 60CSx and Garmin III Handheld Global Positioning System (GPS) navigators (Garmin International, Inc., Olathe, Kansas, USA). If the tortoise was above ground, we recorded whether it was alive or dead. If dead, we studied the carcass and surroundings for indications of the likely cause of death (source of damage to the shell or transmitter, footprints in soil, feces or urine deposits nearby, or digging marks).

Twice each year (spring and autumn), we captured each tortoise to assess its general health (body condition index; Nagy et al. 2002) and vigor, clinical health (disease indicators), body mass (measured to 0.1 g), shell dimensions (measured to 0.1 mm), and to refresh ID numbers and transmitter batteries as necessary. We calculated growth rates of juveniles as the change in MCL (in mm) over a year (autumn to autumn). Sometimes we could not radio-locate released animals at or near their earlier location points. When one became “missing,” we carefully inspected the area and burrow where it was last located for the animal or its carcass, or for other signs, and if that was unproductive, we broadened the search area both visually and electronically. This often led to finding the animal or its transmitter, sometimes far away on top of a hill or at the base of a cliff where Common Ravens (*Corvus corax*) perched or nested. Sometimes we found a missing marked tortoise alive months later, on a subsequent visit. The study sites have been searched multiple times each year since 2005 (this study is still ongoing as of 2013), thus it is likely that tortoises that were still alive, but had failed transmitters, would have been found. Accordingly, we considered still-missing juveniles to have died (termed apparent mortality) at about the time they first disappeared.

Halfway houses.—To test a possible solution to the homing problem, we placed four juveniles inside each of three small predator-resistant enclosures at release sites to allow them to familiarize themselves with the new

area before actual release (i.e., soft release). This procedure has been successfully applied to translocated adult Gopher Tortoises (*Gopherus polyphemus*) where it increased site fidelity and reduced activity areas after release (Tuberville et al. 2005). We compared homing behavior of the halfway-housed juveniles after release to the homing behavior of three groups of five different-sized juveniles (see age/size effects below) that were released around the outside of the halfway houses into burrows we prepared as above. We constructed the fenced and netted portable halfway house enclosures using 5.08 cm galvanized mesh fence (two-inch cyclone fence), galvanized pipe framing, 0.635 cm mesh fence (quarter-inch hardware cloth) footing, with 5.08 cm netting (two-inch-mesh fish netting) over the top (Fig. 1). We erected six cyclone fence panels measuring 1.83 m high and 3 m wide in a hexagonal shape. We attached hardware cloth, 0.9 m wide, vertically to the panels so that a 0.6 m band extended above ground along the base of the fence and a 0.3 m band extended below ground. We attached a horizontal band of aluminum flashing, 0.36 m tall, at the top of the hardware cloth band to deter rodents from entering. The fish net, which was supported by a 3.0 m high central pole with radial cables attached to the side panels, kept out larger birds. We fitted one panel with a door to allow access. We prepared many burrows of different sizes for potential selection by introduced juvenile tortoises within each of these halfway house enclosures.

Homing experiments.—To evaluate the influence of age/size on homing movements following release, we released three groups of five juveniles in September 2005 (Table 1), about six weeks before they were



FIGURE 1. Photograph of Halfway House 3. These enclosures covered 44.9 m² of natural habitat, and housed four juvenile Agassiz's Desert Tortoises (*Gopherus agassizii*) of different sizes and ages from September 2005 to January 2006 to allow them to settle in before being released (via removal of the structure). (Photographed by Ken Nagy).

TABLE 1. Summary of the numbers of juvenile Agassiz's Desert Tortoises (*Gopherus agassizii*) of assorted sizes/ages that were released inside or outside halfway houses (HH) or at the more remote Long Distance Transect (LDT) Site, and the release site distances and compass directions away from the hatchery-nursery enclosures (see site map in Fig. 3), and the seasons of release.

Site	Distance	Direction	Season, year	Number released inside	Number released outside
HH 1	546 m	NNW	Autumn 2005	4	5
HH 2	618 m	NW	Autumn 2005	4	5
HH 3	1030 m	WSW	Autumn 2005	4	5
LDT	1410 m	SSE	Autumn 2005	--	16
LDT	1410 m	SSE	Spring 2006	--	7
LDT	1410 m	SSE	Autumn 2006	--	3

expected to begin brumation (winter inactivity). Each group of five included two small, two year-old juveniles that were in the smallest of the four size groups, plus one juvenile from each of the three larger size groups.

To investigate possible solutions to the problem of homing movements after release, we released all of these juveniles in areas that were out of direct line-of-sight of their natal enclosures (behind low hills). Each of the three release sites was immediately adjacent to one of the three halfway houses. We radio-located and recorded the UTM positions of these 15 juveniles weekly for six weeks, then monthly during winter brumation, then weekly or biweekly through the 2006 spring, summer, and autumn activity season.

In September 2005 (autumn), we placed four tortoises, one from each of the four size groups, inside each of the three halfway houses (Table 1). Each halfway house was adjacent to one of the three sites where five tortoises were simultaneously released (described above), so the five freed tortoises could act as a control group for the four halfway housed experimental group animals. We removed the halfway house structures in January 2006 while the enclosed tortoises were still brumating underground. These juveniles were then radio-located through the 2006 activity season on the same schedule as were the controls.

We evaluated the effect of remoteness of release site on homing efforts by releasing juveniles in September 2005 at four sites. The release sites were located either 546 m NNW (Site HH1; Table 1), 618 m NW (Site HH2), 1030 m WSW (Site HH3), or 1401 m SSE (Site LDT: Long Distance Transect) of the midpoint between the two large hatchery-nursery enclosures. The closest three sites were also the control sites for the halfway housing experiment (see details above). The most

distant site received 16 juveniles, also in September 2005, but this group did not contain any individuals in the largest (141–175 mm MCL, 14–15 y-old) age-size category (none were available). We radio-located the juveniles at the most distant site on the same schedule as the other released juveniles.

Survivorship.—We tested the hypothesis that juveniles released in autumn (September 2005) survived better than those released in spring, by releasing a group of seven juveniles the following spring (May 2006) at Site LDT (Table 1). This group contained an assortment of ages and sizes comparable to the three control groups released in September. Later in 2006, we discovered three more juveniles inside the hatchery-nursery enclosures, and we set them free at the most distant site in October 2006, to participate in our studies of size and age effects on growth and survivorship. We evaluated possible effects of release distance on annual survivorship over three years by using the tortoises involved in the homing and release distance experiments (above). We continued to radio-locate, capture twice annually, and measure these animals during the two years following the end of the homing experiments in winter 2006.

We investigated the influences of age and size on survivorship of all 53 freed juveniles for up to three years after release, until brumation began in 2008. The main criterion for deciding that a missing animal was no longer alive was the continued absence of that juvenile (see details in *Monitoring methods* section above). Plots of survivorship rates (% survival for eight size groups vs. mean MCL of each group at the time of release) were calculated for each of the three years (2006–2008) using cumulative survivorship data.

Statistical analyses.—We used SigmaPlot 12 (Systat Software, Inc., Chicago, IL) with its embedded SigmaStat statistical programs to process and analyze data. We used JMP 8.0 for Mac OS X software (SAS, Cary, North Carolina, USA) to perform logistic regression analyses on growth rates. We evaluated growth of individual tortoises between years using the Kruskal-Wallis test of ranks, and between size groups using One-Way ANOVA followed by Holm-Sidak pairwise multiple comparison test. We tested for an effect of growth rate on survivorship by comparing the previous year's growth of individuals to their survivorship the next year using Nominal Logistic Regression. This procedure was necessary because current year growth could not be determined for animals that did not survive that year. We compared survival between the four groups released at different distances by developing Kaplan-Meier survival curves with staggered entry (Pollock et al. 1989), and evaluated

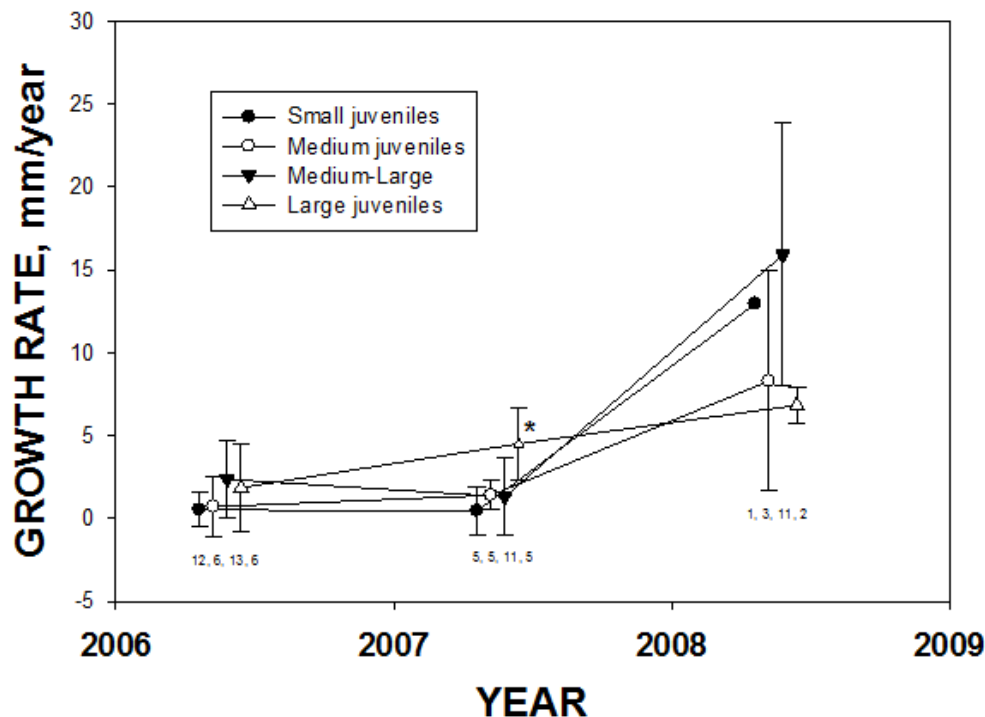


FIGURE 2. Annual growth rates (mean carapace length increase, measured in subsequent Septembers) of four size groups of head-started juvenile Agassiz's Desert Tortoises (*Gopherus agassizii*; MCLs of 45–80 mm, 81–110 mm, 111–140 mm, and 141–175 mm) for each of three years after release. Symbols indicate mean rates, vertical bars are \pm SD, and small numbers below symbols are sample sizes for growth rate determinations. Asterisk indicates large juveniles grew faster in 2007 than did other size groups.

statistical differences between curves using the log-rank test. We accepted statistical significance if $P \leq 0.05$.

RESULTS

Rainfall.—Total rainfall was low during the 2005–2006 period (81 mm; 3.2 inches between 1 July 2005 and 30 June 2006), and even lower in 2006–2007 (22 mm; 0.86 inches). Three sustained rains during autumn and winter of 2007–2008 (totaling 40 mm; 1.57 in) stimulated germination and growth of food plants in late winter and spring 2008, providing annual plant food for juvenile tortoises. Total rain during 2007–2008 was only 41 mm (1.61 in). Average annual rainfall in this part of the Mojave Desert is 75–110 mm (3–4 in; USFWS 2011).

Growth rates.—Annual growth in carapace length by juveniles was slow during the first two years (2005–2007) after release (range for individual animals 0.0 to 8.0 mm/y; Fig. 2), but growth increased significantly the third year (2008; range 6.0 to 31 mm/y, $H = 30.1$, $df = 2$, $P < 0.001$). Growth rates did not differ among the four body size groups in 2005–2006 or in 2007–2008 ($F_{1,15} = 2.11$, $P = 0.161$), but in 2006–2007, juveniles in the largest size group (141–175 mm MCL) grew

significantly faster than tortoises in the other two smaller size groups ($F_{1,25} = 4.23$, $P = 0.017$; see Fig. 2.). Growth rate during 2006 did not significantly affect survivorship during 2007 ($\chi^2 = 1.03$, $P = 0.311$, $n = 40$), and growth rate during 2007 did not significantly influence survivorship during 2008 ($\chi^2 = 2.15$, $P = 0.143$, $n = 29$).

Homing experiments.—Radio-tracking data revealed that all 15 juveniles released in September 2005 moved around and used several burrows before entering brumation four to six weeks later. Most stayed within 150 m of their release sites, but three had moved from 200 to 600 m before brumating. The compass directions of movements for these three animals were not in the homeward direction. The following spring and summer, about half of the juveniles (eight of 15) enlarged their activity areas, and entered brumation in 2006, 13 mo after release. They settled in burrows that were 10 m to 200 m from their release point. Eleven of the 15 juveniles entered brumation burrows in 2006 within 200 m of their 2005 release sites, and one brumated 300 m distant. However, one tortoise released at HH1 had moved 1,050 m east (perpendicular to the compass direction leading to its natal enclosure) before brumation, one juvenile released at HH2 moved 900 m SW (also perpendicular to its homing bearing) and

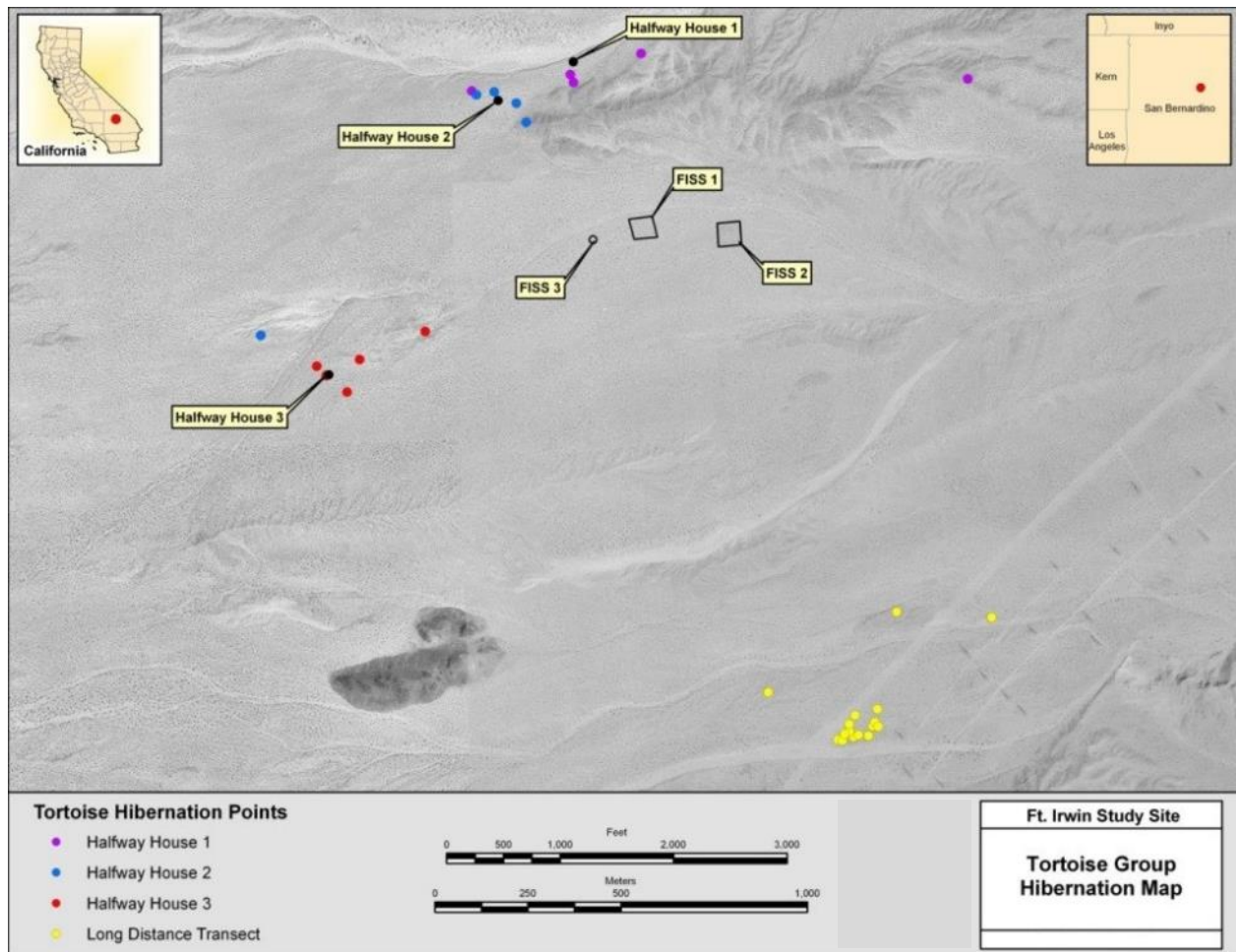


FIGURE 3. Aerial photograph of Fort Irwin Study Site (FISS) area showing locations of the three head-start enclosures (FISS 1, 2 and 3), and the three halfway houses (HH1, 2 and 3). Diagonal lines in lower right are dirt roads. Colored dots show the 2006 over-wintering locations (brumation sites) of Agassiz's Desert Tortoises (*Gopherus agassizii*) released in September 2005 outside HH1 (magenta), HH2 (blue), HH3 (red), and at the most distant site LDT (yellow: released in September 2005 and in spring 2006).

brumated there, and one juvenile released at HH3 moved 300 m toward its natal enclosure before brumating. Inspection of the directionality of the winter burrow positions relative to the release points (Fig. 3) indicates a lack of uniform movement towards the head-start enclosures. None of the 2 to 14 year-old juveniles returned to their natal enclosures, and only one, released at HH3, moved substantially in the direction of their natal enclosures during more than a year of continuous observation. Thus, we observed no age or size effects on homing behavior. After we freed the 12 juveniles from their halfway-houses in January 2006, they remained within 10–200 m of their release points during the 2006 activity season, and none showed an inclination to return to its natal enclosure before entering brumation in autumn.

Thirteen of the 16 juveniles released at the most distant (1.4 km) site (LDT) in September 2005 entered brumation in 2006 within 150 m of their individual release sites, and the remaining three brumated between 200 and 275 m from their release points (Fig. 3). This group of juveniles also did not show directional migration toward their natal enclosures. Thus, there was essentially no homing behavior observed among 43 released juveniles up to 13 mo after their release. In subsequent years, some juveniles dispersed further from their release sites, but the direction of their movements, again, appeared to be random.

Survivorship.—There was no difference in first-year mortality between autumn-released and spring-released juveniles. Twelve-month mortality among autumn-released juveniles at the most distant release site was

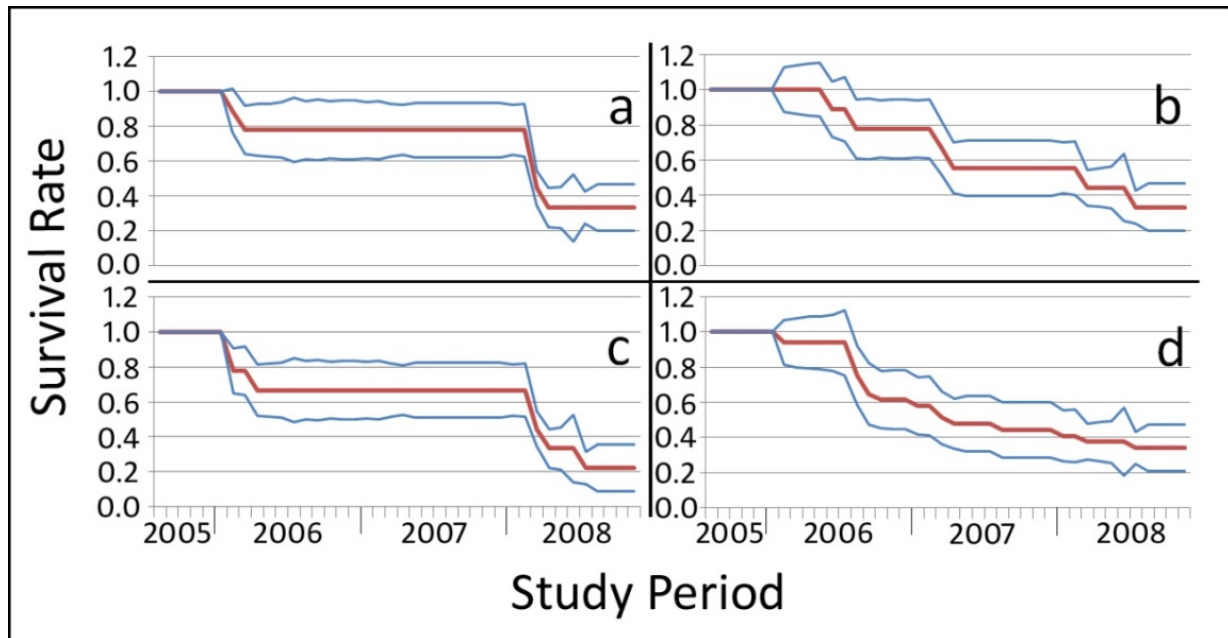


FIGURE 4. Kaplan-Meier survivorship curves with 95% confidence intervals for Agassiz's Desert Tortoises (*Gopherus agassizii*) in the release distance treatment groups: (a) Halfway House 1 at 546 m away; (b) Halfway House 2 at 618 m; (c) Halfway House 3 at 1030 m; and (d) Long Distance Transect at 1410 m.

five out of 16 (31%), and for spring-released juveniles at that site, three out of seven died (43%; $P = 0.657$, Fisher Exact test). Monthly survival rates ranged from 57 to 100% for HH1, 75 to 100% for HH2, 67 to 100% for HH3, and 80 to 100% for LDT treatment groups (Fig. 4), but the survival trends were not statistically significantly different ($\chi^2 = 0.44$; $df = 3$; $P < 0.90$, log-rank test). Inspection of annual survival rates revealed that body size (MCL, mm) was a better predictor of survival than age. After one year, 42 of the 53 released tortoises (79%) were still alive. Most of the apparent mortality in 2005–2006 occurred among the smallest juveniles (Fig. 5), which were all two-year olds when released. In the second year, 32 of the 42 living juveniles (76%) were still alive, and cumulative survivorship had dropped to 60%. Again, most of the apparent mortality occurred among the smallest size categories.

Survivorship increased with shell size and reached 100% at an MCL of just over 100 mm. However, in 2007–2008, the third year, nearly half of the remaining animals apparently died, including all but one of the smallest juveniles, along with many of the largest (Fig. 5). Survivorship for the year was only 53%, and only 32% over the three-year period. In the first year (2005–2006), there was no apparent difference in mortality between the experimental (halfway-housed) and control groups: at Halfway House 1 (HH 1), one control and one experimental juvenile died; at HH 2, no controls and one experimental died; and at HH 3, two controls and one experimental animal died. Thus survival rate was 75%

among halfway-housed tortoises and 80% among free-ranging tortoises; this difference is not statistically significant ($\chi^2 = 0.188$; $df = 1$; $P = 0.665$).

Causes of mortality.—Most deaths were due, or apparently due, to predation. Of the 35 released juveniles that died or presumably died, 32 (91%) were apparently killed by predators, as indicated by forensic evidence. The three non-predator deaths (9%) were due to exposure (carcass undamaged and in a natural posture and location, including two small juveniles dead by apparent freezing in winter and one medium-sized juvenile dead from apparent dehydration in summer). One large juvenile was probably washed away during a flash flood in 2008, and we have been unable to relocate it or its transmitter since then, but it may still be alive. Small juveniles were apparently killed primarily by Common Ravens (Fig. 6). Of the 23 small juveniles that died, two were confirmed as having been depredated by Common Ravens (shells showed characteristic raven damage, carcasses were located beneath raven nesting or roosting sites), and 16 others were strongly suspected to have been taken by Common Ravens. Two small juveniles died from apparent exposure during winter, and three more from predation by unknown species (Fig. 6). Common Raven predation (confirmed and suspected) on small, two year-olds when released, juveniles was moderate to heavy in all three years, eventually leading to nearly complete elimination of that size group (Fig.

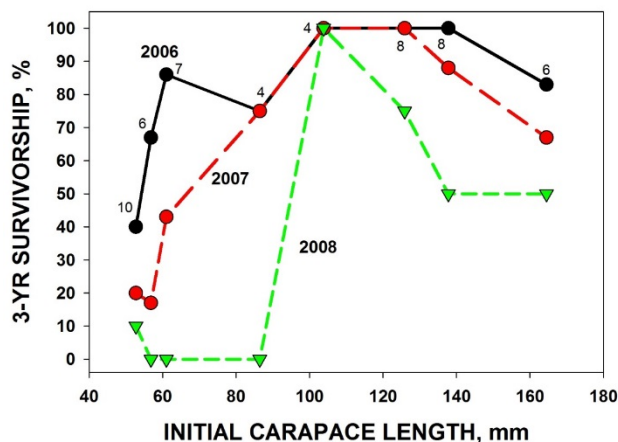


FIGURE 5. Survivorship (percentage of original size group still alive) of 53 juvenile Agassiz’s Desert Tortoises (*Gopherus agassizii*) having various shell sizes at the time of release from a Mojave Desert head-start facility. Small numbers are sample sizes for each size group. The one very small juvenile remaining alive in 2008 (green line) was depredated by a Common Raven (*Corvus corax*) in 2009.

5). Mortality among the larger juveniles was relatively low for two years, but increased greatly during the third year after release (2008), due mainly to Coyote predation (Figs. 5, 6).

DISCUSSION

Homing behavior.—Releasing head-started juvenile tortoises from a hatchery/nursery is a form of translocation. Previous translocations of several species of reptiles have often failed (Dodd and Seigel 1991), and one of the most common causes of failure was homing behavior by released animals (Germano and Bishop 2008), which often ended fatally. Adult Desert Tortoises that were translocated have also been observed to return home or try to do so (reviewed by Berry 1986), and some previously captive tortoises that were released 32 km away from their home pens displayed long-distance, straight-line movements after release consistent with homing, but not in homeward directions, “possibly due to the distance between the (release) site and their former homes” (Field et al. 2007). In fact, an earlier study of homing by juvenile tortoises released at FISS revealed that most juveniles walked toward their home enclosure during the first few days after release (Hazard and Morafka 2002, but see Hazard et al., in press). Accordingly, we expected to see homing efforts by the tortoises we released in this study.

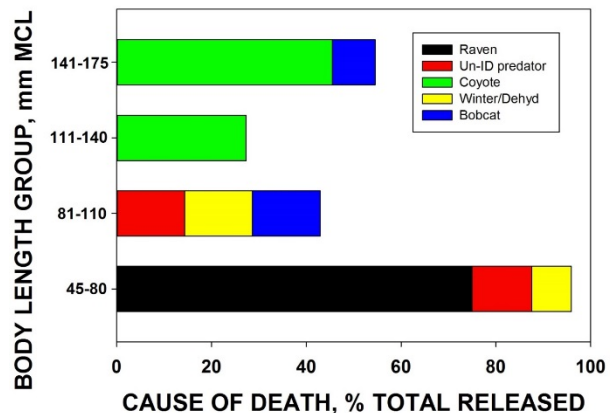


FIGURE 6. Causes of mortality of released juvenile Agassiz’s Desert Tortoises (*Gopherus agassizii*) from 2005 to 2008, shown separately for four body size categories. Each bar segment indicates percent of all tortoises (dead and alive) in that size category, whose death was caused, or apparently caused, by one of the color-coded items listed in the legend (insert). Deaths due to undetermined causes are not shown. All deaths shown were confirmed (carcass found) except for over half of the deaths attributed to Common Ravens (*Corvus corax*) in the smallest size group where carcasses were apparently transported away to remote roosting or nesting sites and deaths are presumed based on strong circumstantial evidence (e.g. transmitter found under known raven perching sites or near fresh raven footprints).

Surprisingly, not one of the juvenile tortoises we released clearly and consistently attempted to walk back to its home enclosure. Homing in head-started tortoises was found by Hazard and Morafka (2002). Their study involved neonate (two month-old) tortoises, which did not attempt to home, and 6–8 y-olds that did home. Our study involved tortoises that were ranged from two to 15 y-olds when released, but only one was in the 6–8 y-old group. Second, although Hazard and Morafka (2002) released tortoises at a similar time of year (October) and used nearly the same protocol as we did, they released animals about 75 m away from, and within sight of, their home enclosures. Hazard and Morafka (2002) speculated that their older juveniles “homed” but the neonates did not because the older animals had gotten over their neonatal urge to disperse, had become familiar with their home area, and had developed site fidelity. If increasing site fidelity with increasing age were an issue, then our eight to 15 y-old tortoises should have shown strong homing movements, but they did not. A new study by Hazard et al. (in press), also conducted at FISS, indicates that juveniles released farther from natal enclosures did not attempt to return home.

Our results indicate that homing behavior of released, head-started juvenile Agassiz’s Desert Tortoises can be minimized, apparently by selecting a release site that is over 500 m from, and not in line-of-sight of, the home enclosures. This strategy apparently worked for tortoises released in autumn and in spring, at release

sites ranging from 540 to 1400 m away, and for a wide range of ages (two to 15-y olds) and sizes (45 to 175 mm MCL) of juveniles. The use of halfway houses to reduce homing behavior was not needed, because in this study, no released tortoises attempted to return home.

Growth.—The low growth rates of small and medium-sized juveniles in the dry years of 2006 and 2007 were similar to those of small juveniles living in another head-start facility called Juvenile Hatchery at Edwards Tortoise Study Site (JHETSS, at the SE corner of Edwards Air Force Base) in 2006 and 2007 (also 1–2 mm/y; Nagy et al., in press). The tortoises at JHETSS, which is located about 128 km (77 mi) WSW of FISS, but still within the Western Mojave Recovery Unit (U.S. Fish and Wildlife Service 2011), also experienced very low rainfall amounts those two years. We expected that those FISS juveniles having zero or negative growth (in carapace length) during 2006 or 2007 would have higher mortality the following year than did those juveniles who were able to grow the previous year. This involves the assumptions that lower growth rates reflected poorer nutrition and probably dehydration (Nagy et al. 1997), and that malnourished and dehydrated juveniles were more vulnerable to dying. However, juveniles having zero or negative growth rates in one year did not have notably higher mortality the year following than did juveniles having positive growth rates that same year. Thus, it appears that poor conditions for growth were not contributing directly to the observed high mortality of the small juveniles at FISS. We noted that different juveniles that hatched in the same year, and even were in the same clutch of eggs, often grew at different rates. We suspect these growth rate differences were due in part to wide variation in food and drinking water availability within pens, and in part to inherent differences in behavior and microhabitat preferences among individuals.

Survivorship.—The relatively low survivorship of the three smallest groups of juveniles, all of which were two year-olds when released, was not surprising. However, these small juveniles fared better than the one year-old tortoises released from the head-start enclosures at Edwards Air Force Base. In six separate release experiments at JHETSS, done in autumns of three years, and including near and far release sites, over 92% of one year-old juveniles were dead within 10 mo of release, mainly from predation by Common Ravens (Nagy et al., in press). Annual mortality of two-year-olds at FISS was much lower, although after three years, accumulated mortality was 96%, also mainly due to Common Raven predation. The remaining two year-old released at FISS was killed by Common Ravens in spring 2009. The complete lack of survival of any of the 23 two year-olds released in this study, while not inconsistent with low

juvenile survivorship observed in long-term field studies of other chelonian species (Brooks et al. 1991; Congdon et al. 1993, 1994), suggests that predation by Common Ravens is a major cause of mortality in the central and western Mojave Desert. Common Raven populations in these parts of the Mojave Desert have increased tremendously due to inadvertent subsidization (increased and stable availability of drinking water and food) by swelling human populations in this desert (Boarman 2003), and ravens are suspected of applying significant predation pressure on tortoise populations where they are subsidized (Kristan and Boarman 2003).

We were surprised by the large increase in predation deaths among the biggest juveniles in 2008. We had assumed that the likelihood of fatal predation decreased with increasing body size and the concomitant increase in effectiveness of basic tortoise anti-predation mechanisms (better “armor”, more wary behavior, harder to obtain a “bite-hold” on bigger tortoises). We had also assumed that shell hardening would limit the probability of predation by Common Ravens on juveniles larger than 110 mm MCL (c.f. Nagy et al. 2011). We had not appreciated the potentially strong influence of drought on predator-prey relationships, particularly those involving Coyote populations. A drought that began in 2006 and extended through most of 2007 apparently led to a widespread increase in predation on large tortoises by hungry Coyotes, whose normal prey base of rabbits, rodents, and small reptiles was drought-depleted. Woodbury and Hardy (1948) suggested that carnivore predation on tortoises may be high during the low points of rabbit population cycles, but did not imply the involvement of drought. Peterson (1994) found high drought-related predation, apparently by Coyotes, in western Mojave tortoises during 1988–1990. Coincident with our study, Esque et al. (2010) found that mortality rates among nine populations of apparently healthy tortoises across the Mojave Desert in California and Nevada, including a population living near FISS, increased from an average of 2% / y in 2006 to 18% / y in 2008.

Hypothesis testing.—Hypothesis (1), that larger juveniles would show stronger homing behavior than smaller juveniles, was not supported: no released juveniles attempted to return to their natal enclosures. Hypothesis (2), that halfway houses would reduce homing behavior, became irrelevant, because no juveniles showed homing behavior at all. Similarly, hypothesis (3), that releasing juveniles at more distant sites would reduce homing, also became irrelevant due to the complete absence of homing behavior. Hypothesis (4) predicted that survivorship among juveniles released in autumn would be higher than among juveniles released in spring. Mortality in both groups during the year following release was substantial

(31–43%), but did not differ significantly between groups, thus failing to support this hypothesis. Hypothesis (5), predicting higher survivorship after release of larger, older juveniles was confirmed: larger juveniles exhibited higher survivorship than smaller juveniles. After three years, the four smallest size (and youngest age) groups combined had only 4% survivorship, while the four largest size and oldest age groups showed 65% survivorship. The largest juveniles may have had even greater survivorship had not unusually strong predation pressure by apparently drought-starved Coyotes occurred in the third year of this study (2008).

Conservation recommendations.—There is controversy about the value of head-starting long-lived turtles and tortoises as a means of increasing population densities (Reed et al. 2009). Protecting tortoises from predation during their vulnerable egg, neonate, and small juvenile stages, then releasing the larger, more predator-resistant juveniles to the wild has been suggested as a recovery management tool (Caporaso 1991; Heppell et al. 1996). However, a sensitivity analysis of population dynamics for Desert Tortoises relative to different management strategies suggested that head-starting alone may not be the most effective approach to increasing population sizes (Reed et al. 2009). That analysis indicated that head-starting was inefficient in promoting population growth compared to enhancing adult female survivorship, and that head-starting efforts would likely yield subsequent population survey results in the short term (25 y) that incorrectly show no increase or even a decrease, due to the combination of normal population dynamics (e.g., size-specific survival rates) and difficulty for survey crews in finding juvenile tortoises. We suggest that head-starting may actually be a preferred recovery tool for stabilizing and increasing tortoise populations in the Western Mojave Recovery Unit, where adult female densities have declined markedly and juvenile tortoises have experienced great predation pressure from Common Ravens. Adult Desert Tortoise density has declined by about 10% per year since 2004 in this Recovery Unit, and there has been a concurrent large drop in the proportion of juveniles in the declining population in this Recovery Unit as well (Roy Averill-Murray, pers. comm.). Densities of adults in the Recovery Unit area west of Highway I-15 apparently have continued to decline, markedly in some places (Berry et al. 2013 and pers. comm.; K.A. Nagy and L.S. Hillard, pers. obs.; E. LaRue, pers. comm.), since the listing of Desert Tortoises as Threatened (FWS 1990) and continuing after publication of the Recovery Plan (FWS 1994). Thus the egg production rate has probably declined substantially as well, rather than stayed the same or increased. This is coupled with possibly complete failure of juvenile survivorship in this

area due to intense predation. Radiotracking studies of head-started one-year-old tortoises released at Edwards Air Force Base revealed 100% mortality following three separate release trials over a four-year period (Nagy et al. in press), and all young (two year-old) tortoises released from the hatchery-nursery facility at Fort Irwin apparently perished (present study). These observations suggest that juvenile tortoise recruitment in the western portion of the Mojave Desert may currently be negligible or even absent due to intense predation exerted by anthropogenically subsidized and enlarged Common Raven populations. Our personal impressions, as long-term observers of neonate and juvenile tortoises living under field conditions in this area, are that spotting young tortoises in the open desert, despite our presumably well-developed search images, have been a rare occurrence for decades. Thus, the strategy of head-starting tortoises to a size that is predator-resistant before release, and/or the use of translocation of adults, may be the only workable options for recovering and sustaining tortoise populations in the western-most part of the Mojave Desert.

In this study, survivorship of released juveniles increased with increasing body size, and reached 100% survivorship (after three years beyond release) at an average body size of about 100 mm MCL. We recommend keeping head-started tortoises inside predator-resistant enclosures until they grow larger than 100 mm MCL. Tortoises in this study developed fully hardened shells when they reached about 110 mm MCL (Nagy et al. 2011), a size at which Common Raven predation apparently declines (Berry 1985). We also recommend releasing head-started tortoises at least 546 m away from the nursery facility, hopefully in a place having an obstructed view of hatchery-nursery enclosures. This may help reduce or eliminate homing behavior and the accompanying increased vulnerability to harm from predators, overheating, and dehydration. Finally, we recommend that focused monitoring of released tortoises, e.g., with radio telemetry, should accompany head-starting efforts in order to evaluate the fate and success of released tortoises, given the difficulties in finding free-living juveniles and the time lag in detecting effects at the population level via traditional survey methods (Reed et al. 2009).

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Clarence Everly for providing Fort Irwin rainfall data, Patricia Nagy, Christiane Weise, and Vaughan Williams for help in the field, and Brian Henen and Lisa Hazard for statistical advice. We also thank Roy Averill-Murray, Kristin Berry, and Ed LaRue for sharing unpublished observations. This research was conducted under permits from the U.S. Fish and Wildlife Service (Native Threatened Species recovery permit TE-085050), the California Department of Fish and Game (Scientific Collecting Permit SC001954), and the UCLA Animal Research Committee (ARC # 1992-057).

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Herpetological Conservation and Biology



KEN NAGY is a Professor Emeritus and a Research Professor in the Department of Ecology and Evolutionary Biology at UCLA, where he has been a faculty member since 1971. A native of Southern California, he received his Bachelor (1967) and Doctor of Philosophy (1971) degrees from the University of California at Riverside, and his doctoral research was on the physiological ecology of the herbivorous desert lizard *Sauromalus obesus* (Chuckwalla). He developed the doubly-labeled water method, which can provide determinations of field metabolic rate, water flux rate, and feeding rate in free-living vertebrate animals, and he applied that technique to wild reptiles, birds, and mammals in various habitats around the world. He summarized his results and those of colleagues in three review publications which present allometric equations (“mouse to elephant curves”) describing field metabolic rates, water influx rates and feeding rates in a large variety of terrestrial animal groupings (taxonomic, dietary, habitat, lifestyle). These empirical equations have been useful for predicting the food, water, and energy needs of species that have not yet been studied in the field. Since retiring in 2006, he has switched his research interests from ecophysiology to conservation biology, especially of Desert Tortoises, and has been conducting tortoise head-starting research on three military bases in the Mojave Desert in California. (Photographed by Brian T. Henen).



MICHAEL TUMA is a professional Wildlife Biologist and Environmental Consultant, and a Ph.D. Candidate at the University of Southern California, where he is pursuing a degree in Integrative & Evolutionary Biology in the Biological Sciences Department. He is investigating the evolution of life-history traits in the North American *Gopherus* tortoises for his dissertation research. As an Environmental Consultant, Mr. Tuma has managed hundreds of projects in over 15 y in the industry. He has a strong working knowledge of the Federal Endangered Species Act and other environmental laws that protects sensitive natural resources, as well as a deep understanding of the processes involved in complying with them. Mr. Tuma’s research interests include population biology, evolutionary ecology, and herpetology. He is particularly interested in the biology of turtles and tortoises, and is actively engaged within the herpetological scientific community. Mr. Tuma is an expert in advanced field data collection and research techniques including translocation, headstarting, radio telemetry, collection of blood and tissue samples, and radiography. He serves as Assistant Editor to the peer-reviewed journal *Herpetological Conservation and Biology*, and has provided peer review for a number of articles for other scientific journals. He is currently pursuing post-doctoral funding for research into the evolutionary ecology and range-wide genetic variation of the east African Pancake Tortoise (*Malacochersus tornieri*). (Photographed by Heather Parks).



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. 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. (Photographed with Bolson Tortoise by Myles Traphagen).



DAVID J. MORAFKA was a herpetologist, a champion of neonatal tortoises, and an inspiring and enthusiastic teacher and colleague who motivated people to achieve goals beyond their own expectations. Dave received a Bachelor’s degree with honors in Zoology in 1967 from the University of California at Berkeley, followed by a Doctor of Philosophy degree in Biology from the University of Southern California in 1974. His academic career began in 1972 at California State University, Dominguez Hills, and later he attained an appointment as a Research Fellow at the Royal Ontario Museum, Toronto, Canada. In 2002, he became a Research Associate at the California Academy of Sciences in San Francisco. He did a lot of research in arid habitats in North America, and authored the book “A Biogeographic Analysis of the Chihuahuan Desert through its Herpetofauna” in 2007. He devoted much effort to reptile conservation (especially Bolson Tortoise and Desert Tortoise head-starting and husbandry), including Desert Tortoise Recovery Team membership, organizing an international symposium on reptile neonatology for Third World Congress of Herpetology, and editorial board memberships with *Chelonian Conservation and Biology*, *Journal of Arid Environments*, and *Herpetological Monographs*. We lost him to cancer in 2004, but his inspiration remains with us. (Photographed by Ken Nagy).