

## EFFECTS OF ARTIFICIAL RAIN ON SURVIVORSHIP, BODY CONDITION, AND GROWTH OF HEAD-STARTED DESERT TORTOISES (*GOPHERUS AGASSIZII*) RELEASED TO THE OPEN DESERT

KENNETH A. NAGY<sup>1,3</sup>, SCOTT HILLARD<sup>1</sup>, STEPHANIE DICKSON<sup>1</sup> AND DAVID J. MORAFKA<sup>2</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, University of California, 621 C.E. Young Drive South, Los Angeles, California 90095-1606, USA

<sup>2</sup>deceased; California Academy of Sciences, San Francisco, California 94118

<sup>3</sup>Corresponding author, e-mail: kennagy@biology.ucla.edu.

**Abstract.**— We subjected neonate Desert Tortoises (*Gopherus agassizii*) that hatched inside fenced, predator-resistant field enclosures containing natural vegetation to either a natural rainfall regime or a regime of natural rainfall plus irrigation (supplemental precipitation) over a five-year period, to test the hypothesis that mimicking an above-average rainfall regime in years of average or low natural rainfall will improve rates of survival and growth. We also tested the hypothesis that survivorship of released 1-yr olds will be high, due to a decline in predation susceptibility once the vulnerable nesting and hatchling phases are completed. Survivorship inside the enclosures during the first year of life was high (averaging 90%) in both groups, even during a record low rainfall year, but growth rates were always substantially higher (2 to 16- $\times$  greater) in rain-supplemented juveniles. Body condition index (CI) measurements indicated that first-year juveniles without added rain were able to maintain body conditions similar to rain-supplemented juveniles during two average rainfall years, but not during a drought year. Older juveniles without added rain died during the latter part of the 16 mo drought, suggesting that the high drought survivorship of first-year non-supplemented juveniles may be related to the yolk they carried after hatching, along with possible behavioral and physiological differences. Nearly all yearlings that were set free (in autumn) were dead within 6 mo, regardless of whether they had supplemental rain or not during their first year inside enclosures, and regardless of whether they were released near the head-start enclosures or a kilometer away. The main cause of mortality was predation, primarily by ravens. The poor survival of released yearling tortoises and the drought-induced death of nearly all older captive juveniles raised without added precipitation lead us to recommend that rain supplementation and delayed release be incorporated in the protocol for head-starting Desert Tortoises.

**Key Words.**—conservation; growth rate irrigation effect; predation

### INTRODUCTION

Mojave Desert populations of the Desert Tortoise (now named Agassiz's Desert Tortoise, *Gopherus agassizii*; Murphy et al. 2011) were listed as Threatened in 1990 due to large declines in population densities (U.S. Fish and Wildlife Service 1994). The revised Recovery Plan (U.S. Fish and Wildlife Service 2008) for the Mojave Desert

population calls for development of protocols and guidelines for population augmentation, including head-starting. The research we report here is part of a larger effort to evaluate and refine the head-starting method (Heppell et al. 1996) for the Desert Tortoise. The primary purpose of head-starting tortoises is to reduce the large losses of eggs and young to predators (Morafka 1994; Morafka et al. 1997). Other goals include reduc-

ing juvenile mortality from drought and starvation (Nagy et al. 1997), monitoring and possibly adjusting sex ratios of hatchlings (Baxter et al. 2008), and evaluating possible introduction and spread of diseases (Jacobson et al. 1991; Brown et al. 1999; Christopher et al. 2003) in head-start facilities.

To further the understanding of the use of head-starting for tortoise survival and conservation, we conducted three experiments. First, we tested the effects of supplementing natural rainfall on annual survivorship, growth rates, and on a body condition index (CI, mainly an indication of hydration level), of tortoises during their first year of life. One group of juveniles (the control) lived in pens receiving only natural rainfall, while a second group (experimental) lived in pens receiving natural rain plus supplemental artificial rain. We irrigated just often enough to maintain the crop of green, growing annual food plants throughout spring, regardless of the amount of natural rainfall.

This was done to mimic but not exceed a good wildflower year in the experimental pens during every year of the five-year experiment. Second, we tested whether tortoises that had received protection from predators for a full year could subsequently survive adequately on their own. In autumn, we released groups of eight yearling tortoises, each carrying a radio transmitter (to enable tracking) to measure survivorship under four conditions: juveniles released near versus far from their head-start enclosures, and juveniles from supplemented versus natural rainfall pens. Third, we tested the hypothesis that water-supplemented juveniles had higher growth rates, CIs, and survivorship than unsupplemented juveniles during their first five years of life. We followed survivorship, growth, and CI of tortoises hatched in 2003, and raised in either supplemented or natural rainfall pens through autumn 2008, when this study ended.

## MATERIALS AND METHODS

**Study site.**—We built three fenced enclosures in open Mojave Desert habitat inside the southeastern corner of Edwards Air Force Base, Los Angeles County, California (34°46.7'N, 117°45.4'W). During installation, we took care to minimize disturbance to the soil and natural vegetation of Creosote Bush (*Larrea tridentata*) and Burro Bush (*Ambrosia dumosa*) living on the previously undisturbed site. We constructed two circular enclosures (10 m radius with a central pole), and a larger tri-lobed enclosure (formed by clustering three circular enclosures together), of cyclone fencing 2 m tall and buried 0.5 m deep. We added a layer of 6 mm-square mesh screen, buried 0.3 m deep and extending 1.5 m high, to the outside of each enclosure to exclude small animals, and later, we installed a layer of shiny metal sheeting 0.5 m high above the mesh screen to exclude climbing rodents (Fig. 1). Netting (5 cm mesh) covered the enclosures to exclude large birds. We divided the large enclosure into three equal areas using galvanized metal flashing buried 0.3 m and rising vertically 0.5 m. We designated one of these three pens as the added rain pen during 2004 and 2005, then we designated a second added rain pen in 2006. Both received added rain in 2006, 2007, and 2008. Irrigation to mimic a rainfall event (supplemental rain) was added in late winter when seed germination of annual plants was either sparse (February 2006) or absent (February 2007), and twice again in spring when annual plants in the added rain pens began to show signs of water stress (wilting, lower leaves turning brown). We sprayed potable city water from a 19047-1 (5,000-gallon) water truck through sprinklers on a central portion of each pen until plastic rain gauges in the pens showed that 25 to 38 mm of water was added. Peripheral parts of each irrigated pen remained dry, so that tortoises therein had a choice of food plants (irrigated and unirrigated).



**FIGURE 1.** Photograph of one of three enclosures at the head-start facility for Desert Tortoises (*Gopherus agassizii*) at Edwards Air Force Base, California, USA.

**Egg procurement.**—We fitted wild adult female tortoises living near the head-start facility with radio transmitters (model AI-2, Holohil Systems Ltd., Carp, Ontario, Canada) and we radio-located them periodically using Lotek receivers (Newmarket, Ontario, Canada). Females used as egg donors were clinically healthy upon field examination and were confirmed to be sero-negative for *Mycoplasma agassizii* antibodies by ELISA tests done on blood samples by Dr. Mary Brown at the University of Florida. When field x-rays (MinXray portable veterinary model HF 8015, Northbrook, Illinois, USA) indicated that females contained eggs at mature stages, we moved females into pens to lay their eggs in prepared burrows, after which we returned females to their home burrows and released them. Egg laying events were indicated by characteristic behaviors and substantial weight losses by females, and confirmed by x-rays. We used most females as egg donors for several years. We surrounded some nests by low plastic fencing where necessary to be sure about the identity of the mother of the emergent hatchlings.

**Hatchling and juvenile measurements.**—We determined the number of eggs each female

deposited in enclosures from x-rays taken before and after laying. We calculated hatching success as:  $100 \times (\text{number of hatchlings subsequently emerging from a nest}) / (\text{number of eggs deposited})$ . We assigned identification numbers to hatchlings (mother's number followed by a dash, then a sequential hatchling number) and marked hatchlings as soon as they emerged from nests. The plastron and 5th vertebral scute were labeled with a permanent ink marker and an epoxy-covered paper tag was attached to the 3rd vertebral scute. We recorded body mass (to 0.1 g, portable digital balance), lengths (midline carapace length or MCL, shell width between the 4th and 5th marginal scutes, and shell height at the same plane as the width measurement, in mm using a digital or analog metric caliper), and calculated body condition index [ $CI = 1000 \times \text{body mass in g} / (\text{MCL} \times \text{shell width} \times \text{shell height, all in mm})$ ; Nagy et al. 2002]. We repeated these measurements at intervals through the active season when juveniles were recaptured. We calculated growth rate as percentage increase in MCL after a year.

**Release experiments.**—In early September, 2004, 4–6 weeks before they would be expected to enter brumation (reptilian hibernation), we recorded the body masses, shell dimensions and CIs of eight yearling tortoises from an enclosure receiving only natural rainfall. We then fitted them with small radio transmitters (Holohil® model BD-2, weighing 2.1 to 2.3 g; 4.7 to 6.1% of juvenile body mass), and weighed them again. We released them just outside their home enclosure, in an effort to minimize possible problems due to any homing behavior (Hazard and Morafka 2002). We designated this experiment 4DN (released in 2004, raised in a dry enclosure, released near their home enclosure). This nearby release location minimized potential problems resulting from any homing behavior (Hazard and Morafka 2002). We released the tortoises at or in burrow entrances we selected from existing, apparently unused natural burrows (prob-

ably dug then abandoned by rodents or lizards) under shrubs, or at new burrows that we dug beforehand. If a released tortoise did not begin using a burrow by late afternoon that day, we placed it in other burrows until it accepted and used one for that night. We monitored released yearlings for several days to insure that each had found a burrow that it used consistently for shelter. In early September 2005, we similarly released a second group of yearling tortoises (designated 5DN). In early September 2007, we did a third release experiment, involving four groups of eight yearlings each: eight tortoises from rain-supplemented pens (designated 7WN; W for wet) and eight more from natural-rain-only pens (designated 7DN) were released near the enclosures to evaluate whether adding precipitation affected survival and growth of released yearlings.

Two more groups of eight yearlings, one from added-rain pens (7WF; F for far) and one from natural rain pens (7DF), were released at an undisturbed site one km south of the head-start facility, in an area having no nearby Joshua Trees (*Yucca brevifolia*) or other high perching sites where ravens or hawks could sit and scan for prey. We radio-tracked transmitted tortoises approximately biweekly during times of the year they might be active (September through mid-November, and mid-February through September), and monthly during the cold of winter (mid-November through mid-February). We periodically recaptured them for measurement of body mass and shell dimensions and for close examination of general health.

**Five-year survivorship and growth.**—We compared survivorship, CI and growth in MCL of the 11 hatchlings emerging in late summer of 2003 in a pen receiving only natural rainfall with the nine hatchlings in an adjacent pen that received both natural and supplemental rain, with the rain supplementation beginning the following spring. We continued measuring survivorship, CI, and growth of these 20 tortoises through September 2008.

**Statistics.**—Results are reported as means along with standard deviation ( $\pm s$ ) and sample size ( $n$ ). Comparisons between treatments were done using t-tests (two-tailed), assuming either equal or unequal variances, as appropriate. Statistical significance was accepted if  $P \leq 0.05$ .

## RESULTS

**Natural rainfall.**—Annual rainfall amounts were close to the long-term average (105 mm) during three of the five years of this study: 2003–2004, 2005–2006, and 2007–2008. Rain during the 2004–2005 season was about three times higher than average (310 mm), and was a record high amount for this area. Two years later, during the 2006–2007 season, rainfall was very low, less than 25% of average, a new record low for this area. The total drought period was 16 months long (May 2006 to September 2007).

**Hatching success.**—We measured nest hatching success during the six years from 2003 to 2008. Predation on eggs and new hatchlings by White-tailed Antelope Squirrels (*Ammospermophilus leucurus*; in 2004) and on un-emerged hatchlings by native Fire Ants (*Solenopsis xyloni*; mainly in 2005) reduced the number of observations we could use to evaluate supplemental rain effects on nest hatching success. During four years when nests were not predated, hatching success of clutches laid in pens having only natural rainfall averaged 76.9% ( $\pm 10.5$ ,  $n = 7$ ) and hatching success in pens that received added rain averaged 66.6% ( $\pm 12.0$ ,  $n = 5$ ). These differences are not significant ( $t = 1.57$ ,  $df = 10$ ,  $P = 0.146$ ). The overall mean hatching success was 72.6% ( $\pm 11.9$ ,  $n = 12$ ).

**Survivorship and body condition of yearlings.**—Heavy predation on hatchlings (as well as on eggs) by ground squirrels in summer 2004, before rodent-resistant flashing was installed on the enclosures, and predation by the Fire Ants whose population erupted

following the high rainfall in 2004–2005, reduced the number of determinations of annual survivorship we obtained for first-year juveniles. Annual survivorship in nine pens having natural rainfall only, over four years, averaged 89.7% ( $\pm 11.7$ ,  $n = 9$ ), while survivorship in added precipitation pens averaged 90.3% ( $\pm 11.6$ ,  $n = 6$ ). These mean survivorship values do not differ significantly ( $t = -0.915$ ,  $df = 13$ ,  $P = 0.915$ ), and the overall mean was 89.9% ( $\pm 11.2$ ,  $n = 15$ ). Survivorship of just those first-year juveniles in three unwatered pens during the drought year (2006–2007) alone was also high (100%, 100%, and 82%), averaging 94.0% ( $\pm 10.4$ ,  $n = 3$ ). Condition Index values of tortoises were usually highest shortly after hatching, and were significantly lower a year later, especially for those juveniles that were still in their first year sometime during the 16-month drought (Table 1). Juveniles living in pens with natural rainfall only had CI values that were the same as those for juveniles in rain-supplemented pens during four of five years. The exception was the drought year, when CIs were 15% lower in pens without supplemental rain (Table 1). The overall average CI of hatchlings was 0.587 ( $\pm 0.038$ ,  $n = 81$ ).

**Growth rates of yearlings.**—During their first year, tortoises living in pens receiving only natural rainfall added 3% to 7% to their shell length per year when rainfall was at or above average (Table 2). However, during the drought year, tortoises that hatched that year in unwatered pens grew little (average 0.8% increase in MCL/yr), and several individuals actually shrunk. Tortoises living in adjacent rain-supplemented pens grew 2–16 times faster (average 6.5). Even during the record high rainfall year, rain-supplementation increased growth rates two-fold.

**Yearling release experiments.**—4DN:Seven of eight yearlings released just outside their head-start enclosures in September 2004 were dead by the following summer: three from predation and four from environmental conditions (winter kill



**FIGURE 2.** Common Ravens (*Corvus corax*) perching on head-start enclosure for Desert Tortoises (*Gopherus agassizii*) with an egg-donor female tortoise in foreground.

during a sudden, early cold period).

5DN:In September 2005, the one released animal still alive was combined with seven more yearlings in a second release experiment that ended by April 2006 with the death ( $n = 6$ ) or disappearance and presumed death ( $n = 2$ ) of all releasees. Of the 15 total released tortoises (4DN and 5DN experiments combined), the probable cause of death of eight tortoises was predation, with seven by ravens that lived in the area and one by a rodent. We did not actually witness deaths, but there were many sources of evidence that implicated ravens. The remains of four more releasees were found, and the proximate cause of their deaths appeared to be freezing, but the ultimate cause of death could not be determined. The other four disappeared under circumstances consistent with predation. Repeated, thorough searching proved fruitless, and they were presumed dead after remaining missing during the next 2.5 yr that researchers continued to work at and around the site.

7WF, 7DF, 7WN, 7DN:We reasoned that raven predation on releasees in 2004 and 2005 was facilitated by elevated perching sites (telephone poles, Joshua Trees, and the enclosures themselves: Fig. 2) near the release sites. To test the hypothesis that survivorship of releasees would

**TABLE 1.** Body Condition Index values from 2003 to 2008 for first-year head-started Desert Tortoises (*Gopherus agassizii*) in the rainfall manipulation experiment enclosure. Values are means  $\pm$  SD, n, along with probability (*P*) values from t-tests comparing dry with wet pens and comparing before and after a year within given pens, or with NS = difference between means is not statistically significant.

Cohort (yr)	When Sampled	CI No Irrigation	CI With Irrigation	<i>P</i>	Annual Rain
2003	Autumn 2003	0.579 $\pm$ 0.048, 11	0.588 $\pm$ 0.031, 7	NS	2003 - 2004 Average
	Autumn 2004	0.511 $\pm$ 0.050, 9	0.520 $\pm$ 0.046, 9	NS	
		<i>P</i> < 0.05	<i>P</i> < 0.05		
2004	Autumn 2004	0.585 $\pm$ 0.031, 7	none		2004 - 2005 Record High
	Autumn 2005	0.543 $\pm$ 0.064, 8	none		
		NS			
2005	Autumn 2005	0.606 $\pm$ 0.036, 4	0.592 $\pm$ 0.042, 9	NS	2005 - 2006 Average
	Autumn 2006	0.411 $\pm$ 0.029, 4	0.422 $\pm$ 0.041, 9	NS	
	Autumn 2007	0.491 $\pm$ 0.043, 10	0.579 $\pm$ 0.029, 18	<i>P</i> < 0.05	2006 - 2007 Record Low
		<i>P</i> < 0.05	NS		
2007	Autumn 2007	none	0.612 $\pm$ 0.034, 15		2007 - 2008 Average
	Autumn 2008	none	0.515 $\pm$ 0.032, 15		
			<i>P</i> < 0.05		



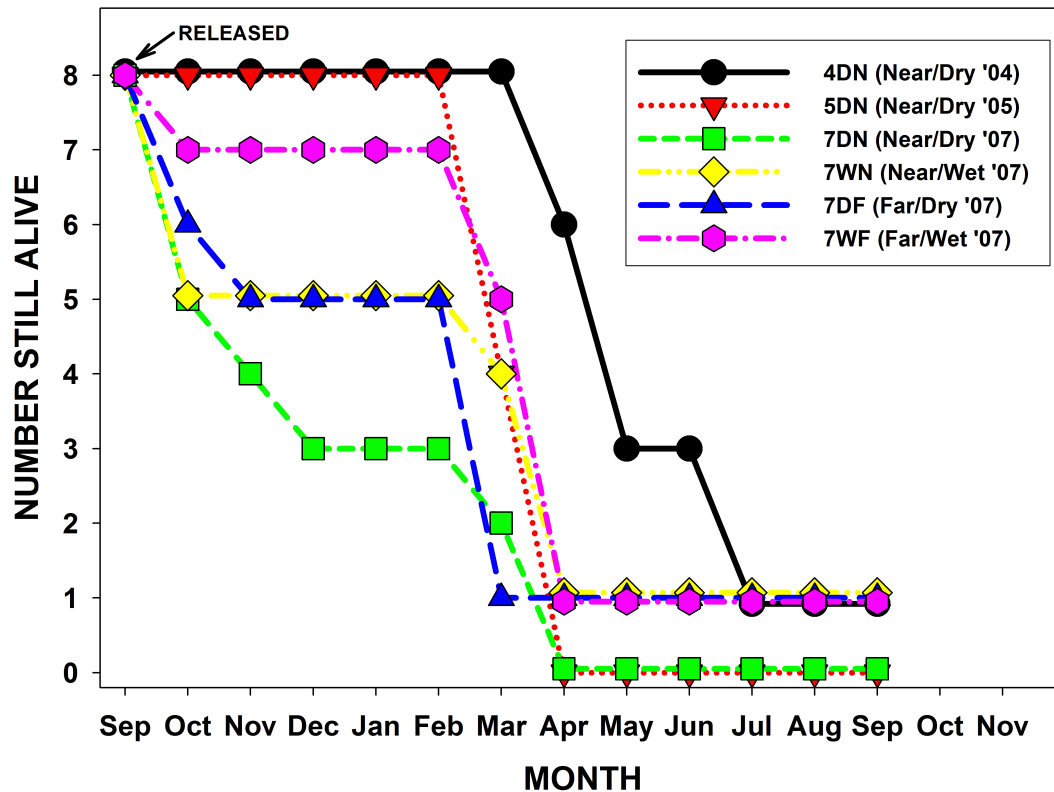
**TABLE 2.** Annual growth rates of yearling Desert Tortoises (*Gopherus agassizii*) living under natural rainfall conditions and with supplemental precipitation in field enclosures containing natural vegetation. Growth was measured as annual percentage increase in midline carapace length (MCL, in mm). Values are means, with standard deviation and sample size in parentheses. (\*2-yr olds: The 2004 cohort of eggs and hatchlings was heavily predated by ground squirrels, and sample sizes were depleted. Instead, growth rates of the 2003 cohort (in their second year) are shown for the 2004–2005 period.

Cohort (year hatched)	Growth rate % per year Natural rain	Growth rate % per year Added precipitation	P ≤	Ratio of Growth rates	Annual Rain
2003	3.34 ± 1.54, 9	18.43 ± 3.61, 7	0.001	5.5	Average
2004*	6.46 ± 3.35, 5	13.56 ± 2.09, 6	0.005	2.1	Record High
2005	6.74 ± 2.10, 4	12.92 ± 4.64, 9	0.007	1.9	Average
2006	0.83 ± 2.06, 10	13.67 ± 3.45, 18	0.001	16.5	Record Low
Average	4.34 ± 2.80, 4	14.65 ± 2.54, 4		6.5 ± 6.87, 4	

be higher if they were released in an area having few or no tall structures, in September 2007 we released two groups of yearlings (eight from watered and eight from unwatered pens) at a site one km away in an area with no nearby fences, poles, or Joshua Trees. As controls, we also released two more groups (eight from watered and eight from unwatered pens) near the enclosures. Twelve of these 32 yearlings were dead within the next three months (Fig. 3). Mortality was absent over winter, but in March, eight more died, and by summer, only three of the 32 releasees remained alive (one 7WN, one 7DF, one 7WF). Clear evidence of raven (and possibly hawk) predation accounted for the deaths of 21 (72%) of the 29 dead releasees. Evidence of avian predation included (1) carcass

or transmitter found under a perching site, often inside an enclosure (having fallen through the bird netting) at the base of a central pole, (2) bird footprints at or near a preferred burrow of a tortoise or at a carcass, and (3) shells opened in a characteristic fashion (hole in middle of plastron or carapace with shell edges bent up around the hole edge). One releasee was apparently killed by a rodent (rodent incisor-shaped tooth marks around shell hole), one died of exposure (transmitter antenna caught on vegetation) and six were missing and presumed dead on the basis of continued absence despite months of careful searching in the surrounding areas.

**Five-year survivorship and growth.**—Predation by ground squirrels (in 2004) and by

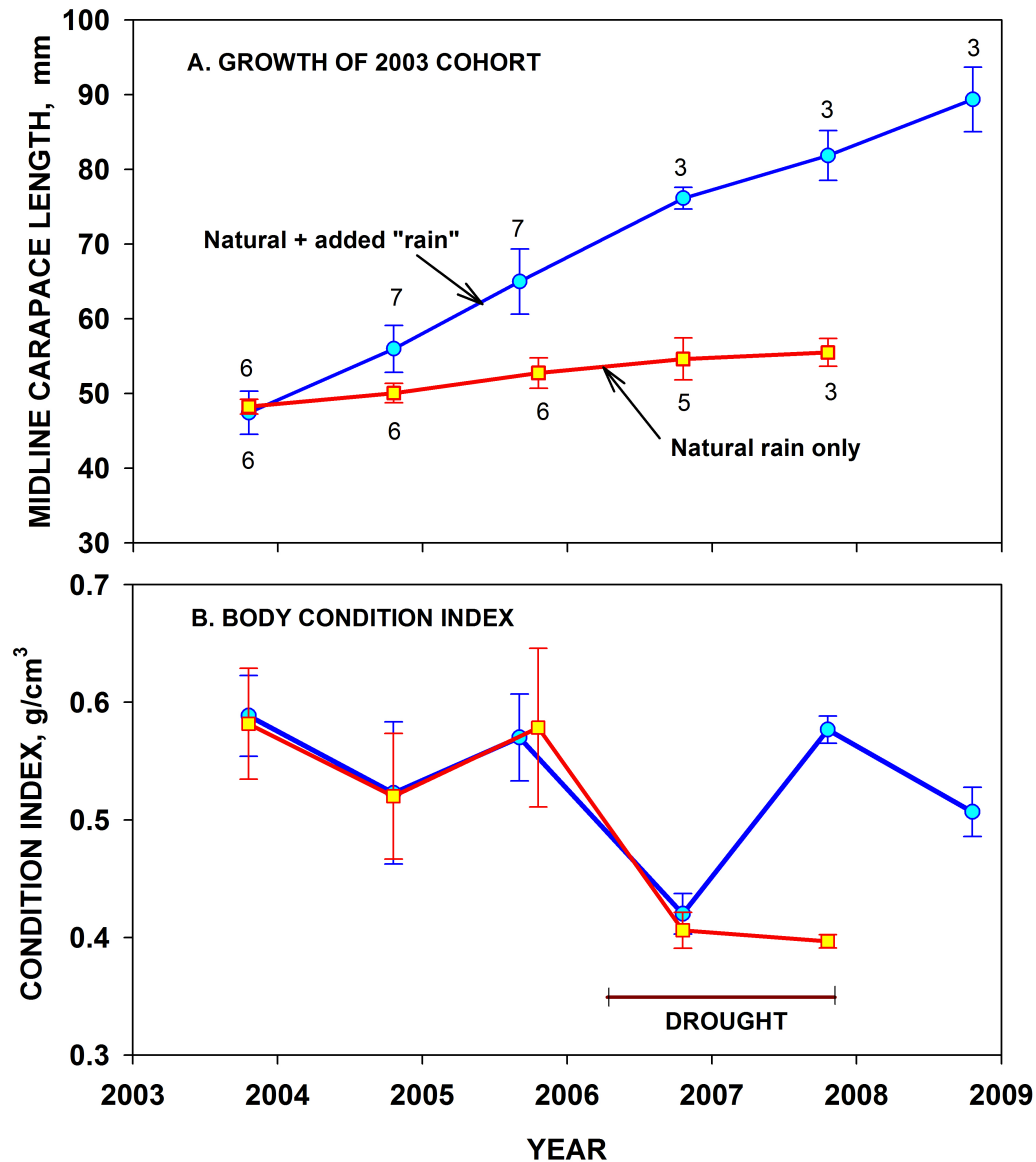


**FIGURE 3.** Survivorship of six groups of eight 1-yr old, head-started Desert Tortoises (*Gopherus agassizii*) all released in early September of three different years (2004, 2005 and 2007). Legend indicates group identity, for example the black line with round symbols represents the 2004 cohort that was raised in a dry pen (natural rainfall only) and was released near that natal pen.

Fire Ants (2005 and 2006) was not restricted to eggs and hatchlings. A squirrel was seen carrying away a yearling tortoise twice in summer 2004 before aluminum flashing was added to the sides of enclosures to exclude rodents. Fire Ants attacked juveniles of all sizes and killed five of the 2003-cohort juveniles in autumn of 2006 (four in the rain-supplemented pen and one in the natural rain pen). The 2003-cohort juveniles that lived under natural rainfall conditions grew much more slowly than did those receiving supplemental precipitation (Fig. 4). After four years, those with natural rain had increased MCL by only 15%, compared to a four-year increase of 73% in length by those

having added precipitation. By the fifth year, added-rain juveniles were 89% longer than they were at hatching, nearly doubling in length. Both groups suffered a large decline in body condition in autumn of 2006, during the drought. But the added-rain group regained good condition the following spring despite the drought; whereas, the body condition of the natural rainfall group continued to decline, and all of these juveniles died of apparent dehydration in summer or autumn of 2007 (Fig. 4).





**FIGURE 4.** Growth (A) and body condition (B) of juvenile Desert Tortoises (*Gopherus agassizii*) hatched in 2003 and living inside head-start enclosures having either natural rainfall only (red lines and symbols) or natural rain plus supplemental precipitation in the form of irrigation (blue lines and symbols) during the next five years. Vertical bars are  $\pm$  standard deviation and numbers are sample size.

## DISCUSSION

We found no significant difference in nest hatching success due to irrigation of enclosures. Unfortunately, a shortage of gravid egg-donor females led to no clutches being laid in unirrigated pens during the drought year (2007), so we have no estimate of hatching success during a severe drought. Hatching success of nests in the two irrigated pens during the drought year were high, averaging 69% and 86%. The overall hatching success of 72.6% that we measured is similar to the values reported from comparable studies: 81.6% in 1998 and 83.0% in 1999 near Twentynine Palms (Bjurlin and Bissonette 2004), and 79% in a head-start facility at Fort Irwin near Barstow (Baxter et al. 2008). Laboratory-incubated eggs from captive female tortoises kept outdoors near Las Vegas had hatching success ranging from 29 to 96%, depending on incubation temperature (Spotila et al. 1994). We conclude that supplementing natural rainfall judiciously, as done in this study, did not influence egg hatching success.

The lack of any significant effect of irrigation on survivorship of juveniles during their first year, especially during the severe drought year, is surprising. Even adult tortoises are known to succumb to drought (Peterson 1994; Berry et al. 2002). Field studies of the water balance of neonate and yearling Desert Tortoises at a head-start facility in the central Mojave Desert (Nagy et al. 1997; Wilson et al. 2001) indicated that a drought year having no available drinking water or green annual plants could be fatal to these young tortoises. Moreover, our observations of the juveniles living in the three unwatered pens during the dry spring and summer of 2007 led us believe they would not live very long. Their CI values had dropped to near or below 0.4, indicating severe dehydration and starvation (Nagy et al., 2002). Most were lethargic and unable (or unwilling) to open their eyes or respond quickly to touch stimuli when encountered at or near their burrow entrances in early

morning and evening. Substantial rain showers in early September ended the drought and apparently saved the lives of those first-year juveniles in the unwatered pens. They drank rainwater, recovered reasonably good body condition by mid-September, and had high annual survivorship (94%). Stored yolk may help confer drought resistance on first-year tortoises (see discussion below).

The judicious addition of supplemental precipitation had a large effect on growth rates of tortoises during their first year. Juveniles in supplemented pens grew much faster than those in pens receiving natural rain only, especially during the drought year, but even during the very wet year. During the high rainfall winter of 2004–2005, germination of annual plants started early due to the large rain in October 2004, and wildflowers were beginning to senesce early, by mid-April, in 2005. Thus, the two irrigation events in the wet pens that spring had a larger than expected effect on prolonging the availability of succulent food that year.

Desert Tortoises can achieve unnaturally high growth rates: up to 176% in their first year (vs. 18% maximum in this study) when fed high quality food and kept in warm conditions all year in captivity, which results in shell and reproductive abnormalities (Jackson et al. 1976). We were careful to avoid producing unusually high growth rates. We adjusted our irrigation events to mimic natural rainfall during an above average rainfall year, by adding about 25 mm of precipitation each time, similar to a shower or thunderstorm in spring, with the number of events per year and the timing of each event being based on the condition of the annual vegetation in the pens. When there was too little rain over winter (2006 and 2007) to initiate natural germination of wildflowers, we irrigated in mid-winter to provide food plants in the supplemented pens. During spring, if food plants in supplemented pens began to dehydrate and wilt, we irrigated as necessary to keep some centrally-located annual plants in each pen green and growing at least until the beginning of June.

We did not irrigate after early June because we did not want to extend the seasonal availability of green vegetation beyond that which wild tortoises would encounter under natural conditions. Annual plants in the western Mojave Desert normally dehydrate and die during June, and both young (Nagy et al. 1997) and adult (Nagy and Medica 1986) tortoises eat dry vegetation (mainly grasses) during summer.

We were not able to reduce the predation pressure on the yearling releasees by rearing them under good growing conditions. The 16 individuals from the added precipitation pens that were relatively large due to faster growth during their first year did not avoid predation any longer than those from natural rainfall pens. Juveniles released in an area with few perching sites for predatory birds also did not fare any better. We agree with Heppell et al. (1996) that the release of head-started tortoises after only one year is too soon for high survivorship. Their small size and soft shells make them easy prey for the many predators in the region, including ravens, hawks, ground squirrels, and native Fire Ants.

Our observation that the 16-month drought of 2006–2007 was fatal to all six of the surviving 2003-cohort (4-yr old) juveniles in the natural-rainfall-only pen is puzzling. The 2006 cohort, which hatched near the mid-point of that drought, survived the drought well, whether they lived in a rain-supplemented or a natural rain pen. We suspect that the large amount of yolk that hatchlings contain in their bodies may help account for their drought-durability. There may also be behavioral differences (remaining in burrows longer, staying inactive, withdrawing into shell) and physiological differences (possible ability to shrink during drought [Wikelski and Thom 2000]; reduced water losses via evaporation [Wilson et al. 2001]) between hatchlings and 4-yr olds that influenced survivorship. To examine this further, we looked at survivorship of other cohorts living in the natural-rain-only pens during the drought period. Drought resistance declined with increasing age:

survivorship through the drought by the 2006 (youngest) cohort was 94%, it was 47% in the 2005 cohort, 50% in the 2004 cohort, and 0 % in the 2003 cohort. These observations indicate that an entire age group of juveniles living under natural rainfall conditions can be killed by a severe drought if the juveniles are around 3–4-yr old. Our results from the irrigated pens show that this can be prevented with supplemental precipitation. Drought-related deaths have been reported in free-living adult Desert Tortoises at two sites in the Mojave Desert of California (Peterson 1994). That drought lasted 31 mo (March 1988 to October 1990), about twice as long as the drought during our study. We suspect that, had the rain storm of 2–4 September 2007 (21 mm total) not happened, many more juveniles in our enclosures would have perished.

**Conclusions and recommendations.**—Head-starting Desert Tortoises in predator-resistant field enclosures containing natural vegetation can greatly reduce juvenile mortality below rates observed outside enclosures. Survivorship of nests and hatching success of eggs can be high, and neonate and juvenile survivorship can also be much higher than they are outside the enclosures. It is necessary to build enclosures that exclude ground squirrels, and native Fire Ant nests may need chemical treatment to reduce above-ground activity if nests increase in activity and number during high-rainfall years. We recommend addition of small amounts of water via sprinklers (20–30 mm per event) as necessary during late winter to initiate annual plant germination in dry winters, and again during spring as needed to keep a patch of annual plants in each pen green until early June. Juveniles should be protected from predators longer than one year before being set free, to improve the probability of their survivorship to adulthood.

**Acknowledgments.**—This research was funded by Department of Defense funds via the U. S. Army National Training Center, Fort Irwin (enclosure construction) and via Edwards Air

Force Base by U.S. Army Corps of Engineers-administered contracts to California State University at Dominguez Hills (Contract DACA09-03-P-0071), and to Tetra Tech Incorporated (subcontracts P50008 and PO60143 to UCLA), and by the Academic Senate and the Department of Ecology and Evolutionary Biology, University of California, Los Angeles. We are grateful to Mickey Quillman, Mark Hagan and Stephanie Pacheco for facilitating funding efforts, Mark Bratton for facilitating field work, the GIS folks at EAFB for aerial photography of the study site, Robert Williams for design and construction of the enclosures, Dr. Gay Naiditch, Dr. Peter Cyog, and Jason Matney at High Desert Animal Care hospital for veterinary advice and x-ray development assistance, Dr Mary Brown and April Johnson at the University of Florida for advice and Melissa Clark, Diana Demcovitz, Janet Stevens, and Diane Heaton-Jones for disease analyses of blood samples at the University of Florida, Roger and Dee at BJ's Water Truck Service in Palmdale, and Mark Bratton, Marcos Mendoza, Patricia Nagy, Ed LaRue, Ingrid and Maury Van der Hope, Christiane Weise, and Vaughan Williams for help in the field, and Dr. Brian Henen and Dr. Russell Burke for much help improving the manuscript. This research was done 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).

#### LITERATURE CITED

- Baxter, P.C., D.S. Wilson, and D.J. Morafka. 2008. The effects of nest date and placement of eggs in burrows on sex ratios and potential survival of hatchling Desert Tortoises, *Gopherus agassizii*. *Chelonian Conservation and Biology* 7:52–59.
- Berry, K.H., E.K. Spangenberg, B.L. Homer, and E.R. Jacobson. 2002. Deaths of Desert Tortoises following periods of drought and research manipulation. *Chelonian Conservation and Biology* 4:436–448.
- Bjurlin, C.D., and J.A. Bissonette. 2004. Survival during early life stages of the Desert Tortoise (*Gopherus agassizii*) in the south-central Mojave Desert. *Journal of Herpetology* 38:527–535.
- Brown, M.B., K.H. Berry, I.M. Schumacher, K.A. Nagy, M.M. Christopher, and P.A. Klein. 1999. Seroepidemiology of upper respiratory tract disease in the Desert Tortoise in the Western Mojave Desert of California. *Journal of Wildlife Diseases* 35:716–727.
- Christopher, M.M., K.H. Berry, B.T. Henen, and K.A. Nagy. 2003. Clinical disease and laboratory abnormalities in free-ranging Desert Tortoises in California (1990–1995). *Journal of Wildlife Diseases* 39:35–56.
- Hazard, L.C., and D.J. Morafka. 2002. Comparative dispersion of neonate and headstarted juvenile Desert Tortoises (*Gopherus agassizii*): a preliminary assessment of age effects. *Chelonian Conservation and Biology* 4:406–409.
- Heppell, S.S., L.B. Crowder, and D.T. Crouse. 1996. Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications* 6:556–565.
- Jackson, C.G., Jr., J.A. Trotter, T.H. Trotter, and M.W. Trotter. 1976. Accelerated growth rate and early maturity in *Gopherus agassizii*. Pp. 99–113 *In* Proceedings of the Desert Tortoise Council, 1976 Symposium. Engberg, N.J., S. Allan, and R.L. Young (Eds.). Desert Tortoise Council, Long Beach, California, USA.
- Jacobson, E.R., J.M. Gaskin, M.B. Brown, R.K. Harris, C.H. Gardiner, J.L. LaPointe, H.P. Adams, and C. Reggiardo. 1991. Chronic upper respiratory tract disease of free ranging

- Desert Tortoises (*Xerobates agassizii*). *Journal of Wildlife Diseases* 27:296–316.
- Morafka, D.J. 1994. Neonates: Missing links in the life histories of North American tortoises. Pp. 161–173 *In* *Biology of North American Tortoises*. Fish and Wildlife Research 13. Bury, R.B., and D.J. Germano (Eds.). U.S. Department of the Interior, National Biological Survey, Washington, D.C., USA.
- Morafka, D.J., K.H. Berry, and E.K. Spangenberg. 1997. Predator-proof field enclosures for enhancing hatching success and survivorship of juvenile tortoises: a critical evaluation. Pp. 147–165 *In* *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles -An International Conference*. Van Abbema, J. (Ed.). New York Turtle and Tortoise Society, New York, New York, USA.
- Murphy, R.W., K.H. Berry, T. Edwards, A.E. Leviton, A. Lathrop, and J.D. Riedle. 2011. The dazed and confused identity of Agassiz's land tortoise, *Gopherus agassizii* (Testudines, Testudinidae) with the description of a new species, and its consequences for conservation. *ZooKeys* 113:39–71.
- Nagy, K.A., and P.A. Medica. 1986. Physiological ecology of Desert Tortoises in southern Nevada. *Herpetologica* 42:73–92.
- Nagy, K.A., D.J. Morafka, and R.A. Yates. 1997. Young Desert Tortoise survival: energy, water and food requirements in the field. *Chelonian Conservation and Biology* 2:396–404.
- Nagy, K.A., B.T. Henen, D.B. Vyas, and I.R. Wallis. 2002. A condition index for the Desert Tortoise (*Gopherus agassizii*). *Chelonian Conservation and Biology* 4:425–429.
- Peterson, C.C. 1994. Different rates and causes of high mortality in two populations of the threatened Desert Tortoise, *Gopherus agassizii*. *Biological Conservation* 70:101–108.
- Spotila, J.R., L.C. Zimmerman, C.A. Binkley, J.S. Grumbles, D.C. Rostal, A. List, Jr., E.C. Beyer, K.M. Phillips, and S.J. Kemp. 1994. Effects of incubation conditions on sex determination, hatching success, and growth of hatchling Desert Tortoises, *Gopherus agassizii*. *Herpetological Monographs* 8:103–116.
- U.S. Fish and Wildlife Service. 1994. Desert Tortoise (Mojave population) Recovery Plan. U.S. Fish and Wildlife Service. Portland, Oregon, USA.
- U.S. Fish and Wildlife Service. 2008. Draft Revised Recovery Plan for the Mojave Population of the Desert Tortoise (*Gopherus agassizii*). U.S. Fish and Wildlife Service. Portland, Oregon, USA.
- Wikelski, M., and C. Thom. 2000. Marine Iguanas shrink to survive El Niño. *Nature* 403:37–38.
- Wilson, D.S., K.A. Nagy, C.R. Tracy, D.J. Morafka, and R.A. Yates. 2001. Water balance in neonate and juvenile Desert Tortoises, *Gopherus agassizii*. *Herpetological Monographs* 15:158–170.



**KENNETH A. 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 Ph.D. (1971) 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 that present allometric equations (“mouse to elephant curves”) 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. Hennen).



**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 agasizii*). 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).





**STEPHANIE DICKSON** attended Scripps College in Claremont California, where she completed her Bachelor of Arts in Biology (2004). She earned her Masters of Arts degree in Biology from the University of California, Los Angeles (2010). Her thesis research focused on the survival rate of head-started yearling Desert Tortoises at Edwards Air Force Base. She received her teaching credential through Rio Salado College (2006) and has developed curriculum and taught middle school science on a variety of topics, including Biology, Chemistry, Forensics, Zoology, Geology, and Physics. She co-authored the Conceptual Physics curriculum for the Higley Unified School District, one of the highest ranked school districts in the state of Arizona. Stephanie has two daughters and lives in Gilbert, Arizona. (Photographed by Ken Nagy).



**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 degree with honors in Zoology in 1967 from the University of California at Berkeley, followed by a Ph.D. 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 much 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).