Journal of Herpetology, Vol. 38, No. 4, pp. 527–535, 2004

Survival during Early Life Stages of the Desert Tortoise (*Gopherus agassizii*) in the South-Central Mojave Desert

CURTIS D. BJURLIN[1] AND JOHN A. BISSONETTE[2]

U. S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit,
Department of Fisheries and Wildlife, Utah State University, Logan, Utah 84322, USA

ABSTRACT.—**Early age classes of the Desert Tortoise (*Gopherus agassizii*) are particularly vulnerable to predation by several mammal and bird species. We studied tortoise survival at the Sand Hill Training Area of the Marine Corps Air Ground Combat Center, Twentynine Palms, California, from 1998 to 1999. We radiographed and thread-spooled 25 females to determine reproductive and nesting ecology. Predators consumed 11 of 42 monitored nests during the first 70 days of incubation. Ninety-one of 132 eggs in nests fenced after 70 days developed into healthy neonates. We recorded 0.84 and 0.91 neonate survival probability during dispersal in 1998 and 1999, respectively. Applying neonatal survival to egg success, we predict that 40% of individuals survived from oviposition to hibernation. Our findings support other chelonian life-history models indicating relatively high mortality early in life. Our data also suggest that neonatal Desert Tortoises are less susceptible to predation than was previously thought, perhaps because of their cryptic coloration and secretive habits. The Common Raven (*Corvus corax*) was not found to be a source of neonate mortality during this study.**

Desert Tortoise (*Gopherus agassizii*) population declines prompted the 1990 decision to list Mojave Desert populations as threatened under the Endangered Species Act (Berry, 1986; U.S. Fish and Wildlife Service, 1994). Baseline data on reproduction and recruitment, however, remain incomplete, hampering construction of reliable life-history models.

Desert Tortoises can live for over 50 years in the wild, but it is unlikely that most reach this age (Germano, 1992). Although recruitment may be as low as 2% (Germano, 1994), this estimate is not well supported, and data on juvenile survivorship is largely anecdotal. Kit Foxes (*Vulpes macrotis*) are implicated as tortoise nest predators (Hampton, 1981; Roberson et al., 1985; Baxter, 1987; Turner et al., 1987) and Common Ravens (*Corvus corax*) as important predators of neonates (Campbell, 1983; Berry, 1985; Farrell, 1989; Boarman, 1992, 1993; Spangenberg, 1996; Karl, 1998). Neither predator, however, has been systematically evaluated for impact on Desert Tortoise survival probability.

The purpose of our research was to quantify Desert Tortoise mortality during the first year of life and evaluate (1) stage-based survival for Desert Tortoise nests, eggs, and neonates; (2) source of mortality; and (3) parental and nest correlates to egg fate. Our data will assist natural resource personnel to develop appropriate management plans, both for this species and potential predators.

MATERIALS AND METHODS

Study Site.—Research was conducted from March 1998 to October 1999 at the Sand Hill Training Area (Sand Hill) in the southwestern corner of the Marine Corps Air Ground Combat Center (MCAGCC), Twentynine Palms, California. Sand Hill is a 99-km^2 non–live-fire range used primarily for personnel and tactical vehicle training. The site is on a bajada of sandy loams (approximately 750 m above sea level) in the foothills of the Bullion Mountains. Perennial vegetation consists primarily of creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and patches of galleta grass (*Hilaria rigida*). Low-density Joshua tree (*Yucca brevifolia*) woodland covers the southwestern corner of the range. Annual grasses and forbs germinate following winter rains (December to March), but unpredictable summer cloudbursts (September) also allow annual plant growth. Average annual rainfall is 81 mm (6–138 mm).

Radiotelemetry of Adults.—We captured and radio-tagged 19 female tortoises in 1998 and six additional females in 1999. Radio-transmitters (AVM Instruments, LTD, type P2-RL) were attached to the first right pleural scute (Boarman et al., 1998). Straight-line maximum carapace length (MCL) was measured during the first visit in the spring and the last visit in the fall and mass was recorded opportunistically throughout the reproductive season (April to July). We worked only with females > 200 mm MCL to maximize

---

[1] Corresponding Author. Present address: Endangered Species Recovery Program, Bakersfield, California, 93304, USA; E-mail: cbjurlin@esrp.csustan.edu

[2] E-mail: john.bissonette@usu.edu

our chance of monitoring those that were reproductively active (Turner et al., 1986; Mueller et al., 1998; Wallis et al., 1999). We estimated age of tortoises by counting scute rings using the methods of Germano (1988, 1998). Tortoises were inspected for upper respiratory tract disease (Jacobson et al., 1991) and cutaneous dyskeratosis (Jacobson et al., 1994). No Sand Hill tortoises appeared diseased.

Radiography and Nest Monitoring.—We radiographed females to determine clutch size and frequency (Gibbons and Greene, 1979) using a portable veterinary x-ray unit (Minxray, Inc., Model X803G), 24 × 30 cm film cassettes (Cronex Quanta III), half-speed blue film (Modern Image), and minimal exposures (60 kV, 25 mA, and 0.1 sec). Females were radiographed on a 10-day schedule but not routinely once calcified eggs were detected. Similar techniques are not thought to affect turtle survival or reproduction (Gibbons and Greene, 1979; Hinton et al., 1997).

Movements and activity patterns of gravid females were monitored with thread-spooling (Scott and Dobie, 1980; Diaz-Paniagua et al., 1995). Tortoises were weighed daily to detect mass loss commensurate with nesting, and suspected nests were located by following thread-trails. Tortoises were frequently found resting at the nest site, and broken, tangled, and buried (individual specific, colored) thread in the nest chamber confirmed that nests were properly attributed to a specific female.

Transfer of human scent to nest sites was reduced by (1) using a plastic ground cloth for sitting and equipment; (2) wearing latex gloves during excavation (nests were located without tools); and (3) altering daily routes to avoid creating scent or visible trails. Because jarring and reorientation of eggs may affect embryo survival (Ewert, 1979), we did not manipulate or uniquely mark eggs prior to incubation. During 1998, we monitored incubating nests weekly from a distance of 10 m, a practice that was discontinued in 1999 to further reduce impact. We considered a nest to be depredated when the general area was disturbed, the nest chamber was exposed, and broken eggshells containing yolk residue were recovered.

After 70 days of incubation, we enclosed nondepredated nests in fencing material to determine egg and nestling fate, and to gain a source of emerging neonates for radiotelemetry. Enclosures were 10 cm high and 30 cm in diameter, constructed of 0.64 cm wire mesh buried to a depth of 3 cm and anchored with stakes of steel reinforcement bar. Because fenced nests may attract predators (Turner et al., 1987), we tested for enclosure effect with 36 mock-tortoise nests baited with chicken eggs. Sham nests were partitioned equally between fenced (treatment) and unfenced (control) groups in a paired design. Three nests, all unfenced, were depredated during the 90-day trial. Although scat deposition at enclosures indicated detection by kit foxes, none of the protected nests were disturbed.

Artificial neonate refugia constructed from PVC pipe (7.6 cm diameter, 20 cm long, split in half longitudinally) were deployed within each enclosure and 5 m from the nest to serve as a soft-release site. Fenced nests were inspected daily, continuing at least three weeks after the emergence of the last neonate. We then carefully excavated and candled remaining eggs (Foust and Riemer, 1986) to confirm status and reburied apparently viable eggs in their original orientation. We successfully tracked the fate of all but five of 202 eggs at known nests. Unknown fate was never attributed to more than one egg per nest, and eggs of unknown fate were excluded from analyses.

Radiotelemetry of Neonates.—All neonates were weighed within 24 h of emergence with an electronic scale (Acculab®, Model PP-150B, ± 0.1 g) and measured with digital calipers (Fowler, Max-Cal, ± 0.1 mm) along maximum carapace length (MCL), width between fifth and sixth marginal scutes, and height between second and third vertebral scutes. Neonates were assigned to two condition groups. Normal individuals appeared healthy, with occasional atypical scute patterns or minor plastron creasing. Abnormal neonates appeared ill (effluent from eyes, yolk scar, cloaca, or mouth), deformed (deeply creased carapace or plastron associated with entombment in the nest), or deficient (incomplete ossification or pigmentation of carapace or plastron).

We used transmitters (Wildlife Materials, Inc., model SOPB-2028, 1.5v, 28 mah silver oxide batteries) to monitor survival and dispersal of 12 and 14 normal neonates in 1998 and 1999, respectively. Complete transmitter packages did not exceed 10% of the recipient's body mass. We fastened transmitters with silicon or epoxy adhesive to the third vertebral scute and immediately released neonates at artificial burrows. We located individuals with handheld radiotelemetry equipment every three days to record health and survival. Transmitters were removed from neonates by 22 and 13 October 1998 and 1999, respectively.

Statistical Analysis.—Tortoises urinate on nests during oviposition and predators may be deterred by the odor of tortoise urine (Patterson, 1971) or the hardened "plug" of soil above the nest chamber as urine dries (Swingland and Coe, 1978). We recorded presence of urine at nest sites and tested whether urine affected nest predation using a *G*-test of independence (Sokal and Rohlf, 1981).

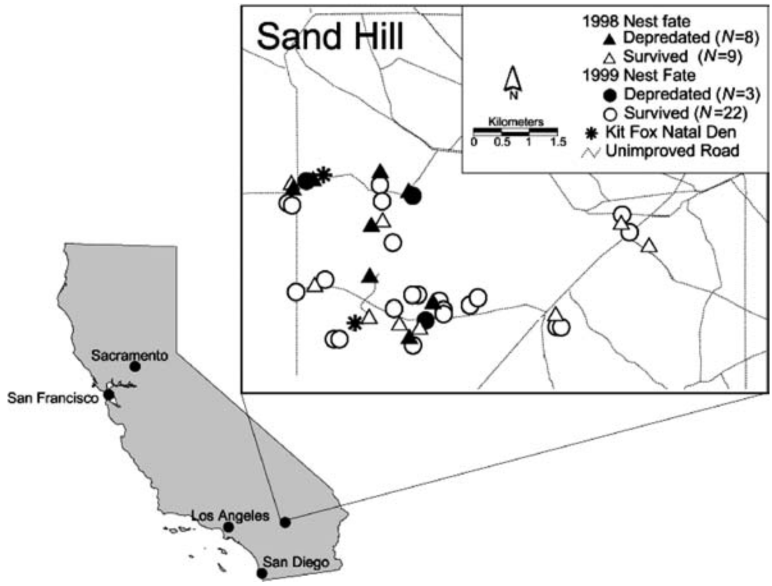

FIG. 1. Spatial distribution and fate of Desert Tortoise nests at Sand Hill, 1998–1999.

Egg hatching and neonate emergence success (normal neonates) from nondepredated nests were examined in relation to maternal MCL and relative egg volume (REV) using Spearman's rank correlation procedures. Because female and egg size may be correlated, we calculated partial correlations between MCL, egg success, and neonate emergence, controlling for REV. We estimated REV using measurements of egg length (L) and width (W) from radiographs, and the following equation for the volume of an elipsoid (Coleman, 1991):

$$\mathrm{REV} = \pi(\mathrm{W}^2)(\mathrm{L})/6.$$

We used the Mann-Whitney *U*-procedure to test for a relationship between clutch size and nest predation. Two-tailed *t*-tests were used to investigate (1) the effect of female MCL on production of abnormal neonates; (2) whether nests with abnormal neonates differed from nests with normal individuals in the number of days needed to complete emergence; and (3) annual differences in neonate size and sibling emergence synchrony. Analyses were conducted using SAS/STAT software, Version 8 of the SAS System for Windows unless otherwise specified and considered significant at $P \leq 0.05$.

We calculated neonate survival probabilities using program MICROMORT v1.3 (Heisey and Fuller, 1985). The program generates maximum likelihood survival probabilities using number of radio-days per interval. This method allowed for staggered entry as neonates emerged from their nests and were outfitted with transmitters. Animals with unknown fate caused by transmitter failure were censured from the population on the last date they were known to be alive. Dispersal interval extended from date of emergence to mid- to late October when spatial movements indicated most neonates had completed autumn dispersal. We applied neonate survival rate during dispersal to the percentage of normal neonates emerging from eggs with known fate to create a survival model for each annual cohort. This model provided an estimate for the likelihood that eggs laid at Sand Hill survived as healthy neonates until the end of autumn dispersal.

RESULTS

Nest Success.—We located 17 of 19 nests created in 1998, and 25 of 30 nests created in 1999 (Fig. 1). Depredation rate was higher in 1998 when 47% of nests were destroyed by predators during the first 70 days of incubation, compared with 12% nest mortality in 1999 (Table 1). Depredated nests were completely consumed with the exception of one that contained a nonviable egg. Kit fox tracks and scat were at most destroyed nests, many of which were located deep within undisturbed tortoise burrows, indicating the predator's diminutive nature. Some depredated tortoise nests were near known kit fox natal dens (Fig. 1), although other nests nearby survived.

Tortoise urine was recorded at 12% and 25% of nests in 1998 and 1999, respectively, and the presence of tortoise urine did not significantly influence nest survival ($N = 41$, $G = 0.02$, df = 1, $P = 0.90$). Two of eight nests with urine were depredated, versus nine of 33 for those without

TABLE 1. Fate of Desert Tortoise nests at Sand Hill, 1998–1999. Subscripts $_{EH}$ and $_{NE}$ denote egg hatching and neotnate emergence, respectively. Nests classified unknown each contained but one egg with undetermined fate but were not depredated and therefore were retained in this table. $\%_{DU}$ excludes depredated and unknown nests.

	1998			1999			1998 + 1999		
Nest fate	*N*	%	$\%_{DU}$	*N*	%	$\%_{DU}$	*N*	%	$\%_{DU}$
Complete $_{EH\ and\ NE}$	5	29.4	62.56	8	32.0	44.4	13	31.0	50.0
Complete $_{EH}$ Partial $_{NE}$	0	0.0	0.0	3	12.0	16.7	3	7.1	11.5
Partial $_{EH\ and\ NE}$	2	11.8	25.0	4	16.0	22.2	6	14.3	23.1
Partial $_{EH}$ No $_{NE}$	0	0.0	0.0	2	8.0	11.1	2	4.8	7.7
No $_{EH}$	1	5.9	12.5	1	4.0	5.6	2	4.8	7.7
Depredated	8	47.1		3	12.0		11	26.2	
Unknown	1	5.9		4	16.0		5	11.9	
Totals	17	100.0	100.0	25	100.0	100.0	42	100.0	100.0

urine. Mean clutch size (± SE) of depredated nests (5.91 ± 0.48), however, was significantly larger than nests that went undetected by predators (4.35 ± 1.31, $Z = 2.77$, $P < 0.01$).

Disregarding depredated nests and those for which egg fate was unknown, 61.5% of 26 nests laid at Sand Hill had total egg hatching success (Table 1). This pattern was similar between years (62.5% of eight nests in 1998, 61.1% of 18 in 1999). However, only 50% of the nests had total neonate emergence as a result of entombment of some nestlings in completely hatched nests during 1999. Of the nests with partial hatching success (30.8%), most produced at least one emergent neonate. Only 8% of nests had partial hatching success with no neonate emergence, and 8% failed to hatch any eggs.

Egg Success.—Depredation destroyed 47 of 85 eggs in 1998 (55.3%), versus 18 of 112 eggs in 1999 (16.1%; Table 2). When depredated eggs were excluded, hatching success for both years was similar (81.6% in 1998, 83.0% in 1999). Neonate emergence (normal and abnormal) also was similar between years but slightly better in 1998 (76.3% in 1998, 73.4% in 1999). We observed individuals in both years that had severe deformities, deficiencies, or illnesses. With abnormal animals excluded, the difference in emergence success between years increased. In 1998, 73.7% of eggs produced normal neonates, compared to 67.0% in 1999 (Table 2). Furthermore, mortality of young within the nest chamber nearly doubled in 1999 (5.3% in 1998 vs. 9.6% in 1999).

One abnormal neonate emerged from each of seven nests (22.6% of 31 nests not depredated during incubation) and no female produced more than one abnormal offspring during the study. Nests yielding abnormal neonates typically had complete hatching success (six of seven nests) but variable emergence. MCL (± SE) was not statistically different ($t = 0.46$, df = 14, $P = 0.65$) between females that produced abnormal neonates (247 ± 4.2 mm, $N = 7$) and those that did not (244 ± 3.7 mm, $N = 11$, represents females with partial to total neonate emergence).

Egg size (REV) averaged over the clutch was not correlated with maternal MCL ($N = 20$, $r = 0.26$, $P = 0.27$). Neither were there correlations of REV on hatching success ($N = 20$, $r = 0.40$, $P = 0.08$) or neonate emergence ($N = 19$, $r = 0.28$, $P = 0.27$) with the influence of MCL removed. Although hatching success was not correlated with MCL ($N = 20$, $r = 0.31$, $P = 0.19$) when the effect of REV was excluded, females larger than 240 mm MCL had increased success and consistency (mean = 0.89, SD = 0.28) compared with smaller females (mean = 0.62, SD = 0.42; Fig. 2A). There was a linear relationship between neonate emergence and maternal MCL ($N = 20$, $r = 0.45$,

TABLE 2. Fate of Desert Tortoise eggs at Sand Hill, 1998–1999. Five eggs with unknown fate were excluded. $\%_D$ excludes depredated eggs.

	1998			1999			1998 + 1999		
Egg fate	*N*	%	$\%_D$	*N*	%	$\%_D$	*N*	%	$\%_D$
Normal neonate	28	32.9	73.7	63	56.3	67.0	91	46.2	68.9
Abnormal neonate	1	1.2	2.6	6	5.4	6.4	7	3.6	5.3
Nestling mortality	2	2.4	5.3	9	8.0	9.6	11	5.6	8.3
Broken	2	2.4	5.3	0	0.0	0.0	2	1.0	1.5
Depredated	47	55.3		18	16.1		65	33.0	
No development	3	3.5	7.9	12	10.7	12.8	15	7.6	11.4
Developed and died	2	2.4	5.3	4	3.6	4.3	6	3.0	4.5
Totals	85	100.0	100.0	112	100.0	100.0	197	100.0	100.0

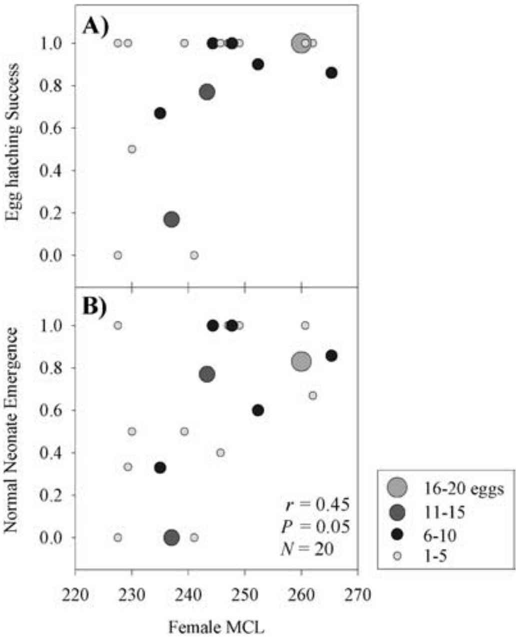

FIG. 2. Correlation between female maximum carapace length (MCL) and egg hatching success (A) and neonate emergence (B) for nondepredated nests at Sand Hill, 1998–1999. Bubbles represent all eggs for females in both years, with size corresponding to number of eggs.

$P < 0.05$) with the influence of REV removed (Fig. 2B).

Neonate Size and Emergence.—We measured 28 and 63 normal neonates in 1998 and 1999, respectively. Weight ($t = 4.8$, df = 89, $P < 0.001$), MCL ($t = 5.0$, df = 89, $P < 0.001$), and width ($t = 2.2$, df = 89, $P < 0.03$) were significantly larger in 1999, but there was no difference in neonate height between years (Table 3).

Siblings emerged synchronously. Emergence was infrequently completed on day one (8.7% of 23 nests), but many nests had completed emergence on day two (30.4%), day five (17.4%), or day seven (13.0%; Fig. 3A) of activity. The first neonates to emerge generally appeared healthy, whereas neonates with greatly delayed emergence often were abnormal (Fig. 3B). Nests containing abnormal neonates were significantly less synchronous ($t = 3.34$, df = 5.37, $P = 0.02$, mean = 11.5 days between exit of first and last neonate, SE = 2.43, $N = 6$) than those with healthy neonates (mean = 3.2 days, SE = 0.47, $N = 17$; Fig. 3B).

Survival Model.—We tracked 26 neonates for 787 radio-days in 1998–1999, during which two animals were recovered dead (Table 4). An unidentified predator took one in 1998 and another died of unknown causes (not depredation) shortly after release in 1999. Mean survival probability for healthy neonates during the dispersal interval was 0.88 (0.84 for 1998, and 0.91 for 1999).

TABLE 3. Neonate morphometrics (Mean ± SD) within 24 h of emergence from the nest and Sand Hill, 1998–1999.

	1998	1999	1998 + 1999
N	28	63	91
Weight (g)	19.4 ± 2.17	22.2 ± 2.78	21.3 ± 2.91
(Range)	(15.5–23.7)	(14.4–28.2)	(14.4–28.2)
Length (mm)	42.3 ± 1.55	44.4 ± 2.05	43.8 ± 2.15
(Range)	(37.6–44.8)	(37.0–48.7)	(37.0–48.7)
Width (mm)	36.9 ± 1.47	37.9 ± 2.17	37.5 ± 2.03
(Range)	(34.0–39.4)	(32.1–42.4)	(32.1–42.4)
Height (mm)	22.2 ± 1.82	22.4 ± 1.52	22.3 ± 1.60
(Range)	(19.7–29.1)	(19.5–26.2)	(19.5–29.1)

Combined survival of nests, eggs, and neonates suggests a pattern of decreasing mortality by life stage (Fig. 4) in which an estimated 40% of the eggs laid by Sand Hill females survived as healthy neonates to hibernation (mid-October). There was, however, considerable annual variation in survival probability (28% in 1998 and 51% in 1999) in large part because of a pulse of heavy nest predation in 1998.

DISCUSSION

Nests.—Nest depredation is highly variable among sites and years. Rates for the Desert Tortoise vary from 13% (Hampton, 1981) in the western Mojave Desert to 63% (Karl, 1998) and 70% (Roberson et al., 1985) in the eastern Mojave Desert. Roberson et al. (1985) found that 42% of 26 tortoise nests were depredated a few hours after oviposition, but this pattern was not observed at Sand Hill. In 1998, only one nest was destroyed during the first week of incubation, whereas all other depredations occurred in early August, more than one month after nesting.

Our estimate of 26% nest depredation at Sand Hill appears relatively low for Desert Tortoise populations. During 1998 when we visited nests weekly, most predation events occurred in a single pulse. In 1999, we visited nests twice, once to locate and once to enclose after 70 days of incubation. The dramatic decrease in depredation (47% in 1998 vs. 12% in 1999) suggests that weekly monitoring may facilitate predator detection of tortoise nests, despite precautions to reduce impact. Our observations lead us to question the accuracy of previous nest survival estimates for the Desert Tortoise. Although flag markers at bait and census stations did not increase visitation by predators at a turtle nesting area (Tuberville and Burke, 1994), we believe that a systematic study of researcher impact on predator behavior is warranted. Surveyors currently take no precautions to reduce human scent

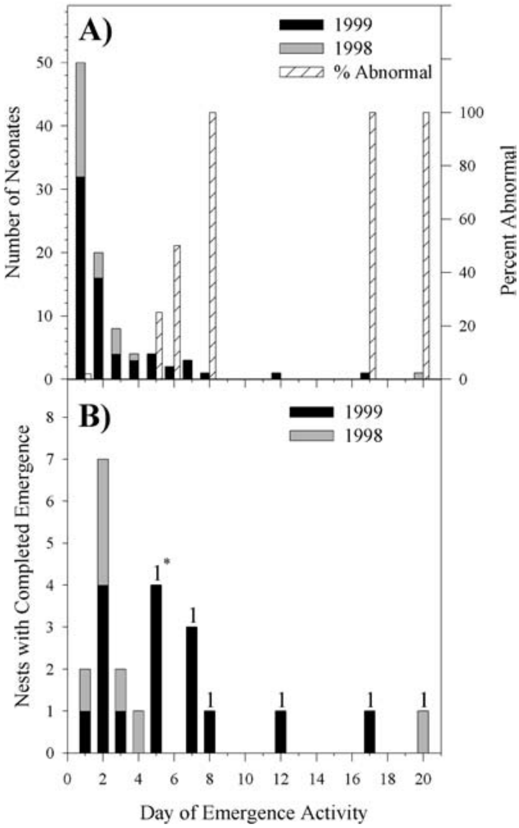

FIG. 3. Number of days for complete emergence of nests (A) and emergence synchrony for Desert Tortoise neonates (B) and at Sand Hill, 1998–1999. Emergence activity was considered to begin when the first neonate from each nest was located within the enclosure. Percent Abnormal includes all deformed, deficient (pigment abnormalities, incomplete shell ossification), or ill (nasal, oral, or ocular effluent) animals. * Bar headers in (A) indicate number of nests containing an abnormal neonate. $N = 23$ nests, 98 neonates.

at burrows, potentially affecting survival of tortoises and their nests.

Some predators appear deterred by tortoise urine (Patterson, 1971), but urine soaked nests were not at lower risk of predation during this study. Sand Hill received summer precipitation in 1998 and 1999 that saturated the top centimeters of soil, possibly overwhelming the influence of urine. We believe that voiding, however, is simply an involuntary side-effect of oviposition that plays no adaptive role in protecting tortoise nests.

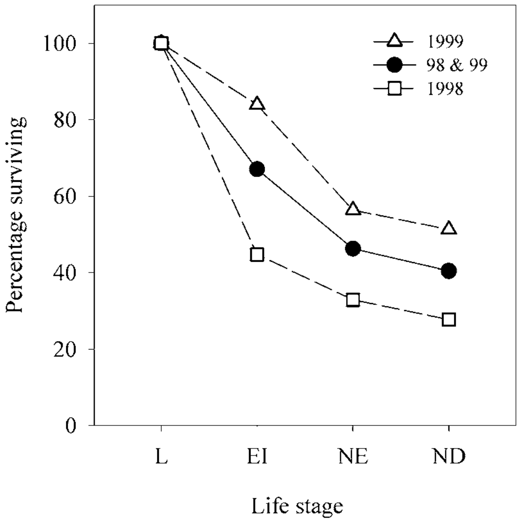

FIG. 4. Percentage of tortoises surviving by life stage at Sand Hill, 1998–1999. After egg laying (L), mortality began during egg incubation (EI) when nests were depredated, and continued during neonate emergence (NE) and neonate dispersal (ND).

Although cues used by predators remain unverified, larger clutches may have been at greater risk of predation as a result of increased metabolic activity and odors. Alternatively, it may be difficult for female tortoises to deposit large clutches without damaging eggs. The only 1998 nest at Sand Hill that was depredated during the week after oviposition contained seven eggs, two of which were broken. We located broken eggs in two additional nests with clutch sizes of four and six; the latter was depredated. Other broken eggs likely went undetected because our protocols precluded complete nest excavation. Roberson et al. (1985) reported natural breakage in 6.6% of 61 Desert Tortoise eggs but did not report effects on depredation.

Eggs and Nestlings.—The two previous studies that reported hatching success of wild Desert Tortoise nests had conflicting results. Turner et al. (1986) monitored 57 eggs at Goffs, California, in the Mojave Desert, recording 45.6% emergence from the nest, 38.6% late-term egg death, and

TABLE 4. Survival probabilities for normal neonates during autumn dispersal at Sand Hill, 1998–1999.

Year	N	Interval length (days)	Radio-days	No. deaths	Daily		Interval	
					Survival	95% CI	Survival	95% CI
1998	12	57	319	1	0.997	0.991–1.000	0.836	0.588–1.000
1999	14	46	468	1	0.998	0.994–1.000	0.906	0.747–1.000

15.8% nondevelopment. McLuckie and Fridell (2002) reported 73% hatching success on the Beaver Dam Slope of Utah but did not identify the fate of other eggs. At Sand Hill, egg hatching success (82.5%) and neonate emergence (74.2%) was considerably higher than reported by Turner et al. (1986) but consistent with McLuckie and Fridell's data.

Although nestling death has not been reported frequently for Desert Tortoises (but see Karl, 1998), 10% of 109 hatchlings at Sand Hill were found trapped or dead in the nest. Moisture-laden soils may have negatively affected neonate emergence, and consequently survival. Rainfall during the incubation period was nearly twice the normal level (56.6 mm in 1998 and 60.7 mm in 1999, vs. 18 yr mean of 31.1 mm) and nests were saturated during emergence in 1999 when entombment was at its highest (9.6% in 1999 vs. 5.3% in 1998).

Female size was positively correlated with neonate emergence success at Sand Hill. Nearly half the females for which we recorded egg fate were smaller than 240 mm. These individuals likely were relatively young and still growing (Germano, 1994), potentially affecting offspring survival. An alternative explanation is that large females produce larger eggs, and consequently more robust neonates. Egg volume, however, was not correlated to female size or neonate emergence at Sand Hill. Regardless of the cause, increased neonate emergence for large females is remarkable because it is complementary to the positive correlation between clutch size and female size reported at several sites (Turner et al., 1986; Mueller et al., 1998; Wallis et al., 1999). Increased annual egg production and neonatal success identify the relative importance of large females to population growth rate.

Neonate Emergence and Survival.—Newly hatched tortoises bear an external yolk sac that makes movement difficult for one or more days after pipping (Woodbury and Hardy, 1948; Booth, 1958; Morafka, 1994). We did not observe external yolk sacs on Sand Hill emerged neonates, indicating that young pipped and stayed within the egg or nest chamber for at least 24h while absorbing yolk.

Few Desert Tortoise neonates at Sand Hill died during autumn dispersal, but this may not have been the period of greatest mortality. Dispersing neonates typically remain under the cover of vegetation or in subterranean burrows, with concomitant reduction of predation risk. The scenario likely reverses in spring when neonate yolk energy has been expended, annual forbes and grasses are generally plentiful, and predators are active and breeding (Nagy et al., 1997). Overwintering and spring survival of yearling Desert Tortoises is currently unreported, but remained relatively high during research that the primary author recently concluded at a nearby site in the foothills of the little San Bernardino Mountains (CDB, unpubl. data).

The Common Raven (*Corvus corax*) is thought to be an important predator of juvenile Desert Tortoises (Berry, 1985; Boarman 1992, 1993; U.S. Fish and Wildlife Service, 1994). Ravens were observed at Sand Hill throughout the study and flocks of 15–60 individuals frequently coexisted with radio-tagged neonates during September in both years. However, we did not find evidence that tagged neonates were killed by ravens.

Patterns of Tortoise Survival.—When placed on a lifelong abscissa, our data appear to support Iverson's (1991) assessment that Desert Tortoise survival fits a type III curve with relatively high mortality early in life. Although the effects of researcher activity on tortoise nest predation remain unclear, the widely accepted paradigm that nests are a uniquely vulnerable stage in chelonian life history (for reviews, see Wilbur and Morin, 1988; Iverson, 1991) was supported by this study. Dispersing Desert Tortoise neonates may be less susceptible to predation than was previously thought, however, in part caused by cryptic coloration and behavior. These data appear to support a predator avoidance hypothesis over a low-survival hypothesis to explain infrequent detection of neonates during walking surveys. Survival at Sand Hill and elsewhere certainly will fluctuate among years depending upon availability of forage, rainfall, predators, and humans. Additional studies of nest and neonate survival are warranted.

Management programs for the Desert Tortoise have suffered from a lack of reliable information for early life stages. In addition to providing data for the production of tortoise life-history models, our results illustrate the need for better techniques for detecting young tortoises during surveys. Furthermore, the absence of raven predation on neonates at Sand Hill warrants reevaluation of the data that have resulted in raven control and numerous policy publications.

Acknowledgments.—The U.S. Marine Corps at Twentynine Palms, California, and a Presidential fellowship and G. Smith scholarship from Utah State University supplied funding for this research. Southwest Division, Naval Facilities Engineering Command provided technical support. We thank A. Wells, E. Punkay, B. Joy, D. Griffin, S. Jones, W. Fisher, R. Evans, C. White, and T. Griffin for field or administrative assistance. We thank D. Rakestraw, K. Rautenstrauch, J. Mueller, D. Morafka, J. Lovich, W. Boarman, B. Henen, and K. Berry for instruction in field techniques and research suggestions. S. Durham provided valuable statistical support. S. D. Busack, E. Brodie Jr.,

T. Crowl, and B. Cypher reviewed versions of this manuscript. We received indispensable x-ray equipment and developing facilities from Merry X-ray (Salt Lake City, UT), Modern Image X-ray (Salt Lake City, UT), and High Desert Medical Center (Joshua Tree, CA). Gutermann Thread Company (New York, NY) donated over 50 miles of sewing thread for tracking tortoises to nesting sites. All research was conducted in accordance with USFWS endangered species permit PRT-839235 and Utah State University animal use and care permit IAUC 906.

LITERATURE CITED

BAXTER, R. J. 1987. Analyses of the Population and Spatial Distribution of the Desert Tortoise (*Gopherus agassizii*) at the Twentynine Palms Marine Corps Base. Unpubl. master's thesis, California State Polytechnic Univ., Pomona.

BERRY, K. H. 1985. Avian Predation on the Desert Tortoise (*Gopherus agassizii*) in California. U.S. Bureau of Land Management, Riverside, California. Report to Southern California Edison Co., Rosemead.

———. 1986. Desert Tortoise (*Gopherus agassizii*) research in California, 1976–1985. Herpetologica 42:62–67.

BOARMAN, W. I. 1992. Problems with management of a native predator on a threatened species: raven predation on desert tortoises. *In* J. E. Borrecco and R. E. Marsh (eds.), Proceedings of the 15th Vertebrate Pest Conference, pp. 48–52. Univ. of California, Davis.

———. 1993. When a native predator becomes a pest: a case study. *In* S. K. Majumdar, E. W. Miller, D. E. Baker, E. K. Brown, J. R. Pratt, and R. F. Schmalz (eds.), Conservation and Resource Management, pp. 191–206. Pennsylvania Academy of Science, Easton.

BOARMAN, W. I., T. GOODLETT, G. GOODLETT, AND P. HAMILTON. 1998. Review of radio transmitter attachment techniques for turtle research and recommendations for improvement. Herpetological Review 29:26–33.

BOOTH, K. 1958. Development of eggs and young of Desert Tortoise. Herpetologica 13:261–263.

CAMPBELL, T. 1983. Some natural history observations of Desert Tortoises and other species on and near the Desert Tortoise Natural Area, Kern County, California. Proceedings of the Desert Tortoise Council Symposium 1983:80–88.

COLEMAN, R. M. 1991. Measuring parental investment in nonspherical eggs. Copeia 1991:1092–1098.

DIAZ-PANIAGUA, C., C. KELLER, AND A. C. ANDREU. 1995. Annual variation of activity and daily distances moved in adult spur-thighed tortoises, *Testudo graeca*, in southwestern Spain. Herpetologica 51:225–233.

EWERT, M. A. 1979. The embryo and its egg: development and natural history. *In* M. Harless and H. Morlock (eds.), Turtles: Perspectives and Research, pp. 333–413. John Wiley and Sons, New York.

FARRELL, J. P. 1989. Natural history observations of raven behavior and predation on Desert Tortoises. Proceedings of the Desert Tortoise Council Symposium 1989:168.

FOUST, A., AND D. N. RIEMER. 1986. Candling turtle eggs. Herpetological Review 17:43–44.

GERMANO, D. J. 1988. Age and growth histories of Desert Tortoises using scute annuli. Copeia 1988:914–920.

———. 1992. Longevity and age-size relationships of populations of Desert Tortoises. Copeia 1992: 367–374.

———. 1994. Comparative life histories of North American tortoises. *In* R. B. Bury and D. J. Germano (eds.), Biology of North American Tortoises, pp. 175–185. Fish and Wildlife Research 13, Washington, DC.

———. 1998. Scutes and age determination of Desert Tortoises revisited. Copeia 1998:482–484.

GIBBONS, J. W., AND J. L. GREENE. 1979. X-ray photography: a technique to determine reproductive patterns of freshwater turtles. Herpetologica 35:86–89.

HAMPTON, A. M. 1981. Field studies of natality in the Desert Tortoise. Proceedings of the Desert Tortoise Council Symposium 1981:128–138.

HEISEY D. M., AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

HINTON, T. G., P. D. FLEDDERMAN, J. E. LOVICH, J. D. CONGDON, AND J. W. GIBBONS. 1997. Radiographic determination of fecundity: is the technique safe for developing turtle embryos? Chelonian Conservation and Biology 2:409–414.

IVERSON, J. B. 1991. Patterns of survivorship in turtles (order *Testudines*). Canadian Journal of Zoology 69:385–391.

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.

JACOBSON, E. R., T. J. WRONSKI, J. SCHUMACHER, C. REGGIARDO, AND K. H. BERRY. 1994. Cutaneous dyskeratosis in free-ranging Desert Tortoises, *Gopherus agassizii*, in the Colorado Desert of southern California. Journal of Zoo and Wildlife Medicine 25:68–81.

KARL, A. E. 1998. Reproductive Strategies, Growth Patterns, and Survivorship of a Long-Lived Herbivore Inhabiting a Temporally Variable Environment. Unpubl. Ph.D. diss., Univ. of California, Davis.

MCLUCKIE, A. M., AND R. A. FRIDELL. 2002. Reproduction in a Desert Tortoise (*Gopherus agassizii*) population on the Beaver Dam Slope, Washington County, Utah. Chelonian Conservation and Biology 4:319–329.

MORAFKA, D. J. 1994. Neonates: missing links in the life histories of North American tortoises. *In* R. B. Bury and D. J. Germano (eds.), Biology of North American Tortoises, pp. 161–173. U.S. National Biological Service of the Fish and Wildlife Resources, No. 13, Washington, DC.

MUELLER, J. M., K. R. SHARP, K. K. ZANDER, D. L. RAKESTRAW, K. R. RAUTENSTRAUCH, AND P. E. LEDERLE. 1998. Size-specific fecundity of the Desert Tortoise (*Gopherus agassizii*). Journal of Herpetology 32: 313–319.

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.

Patterson, R. 1971. The role of urination in egg predator defense in the Desert Tortoise (*Gopherus agassizii*). Herpetologica 27:197–199.

Roberson, J. B., B. L. Burge, and P. Hayden. 1985. Nesting observations of free-living Desert Tortoises (*Gopherus agassizii*) and hatching success of eggs protected from predators. Proceedings of the Desert Tortoise Council Symposium 1985:91–99.

Scott, A. F., and J. L. Dobie. 1980. An improved design for a thread trailing device used to study terrestrial movements of turtles. Herpetological Review 11: 106–107.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co., New York.

Spangenberg, K. E. 1996. Field Enclosures: Their Utility in Life History Studies and Conservation of Juveniles of the Desert Tortoise (*Gopherus agassizii*). Unpubl. master's thesis, California State Univ., Dominguez Hills.

Swingland, I. R., and M. Coe. 1978. The natural regulation of giant tortoise populations on Aldabra Atoll. Reproduction. Journal of Zoology (London) 186:285–309.

Tuberville, T. D., and V. J. Burke. 1994. Do flag markers attract turtle nest predators? Journal of Herpetology 28:514–516.

Turner, F. B., P. Hayden, B. L. Burge, and J. B. Roberson. 1986. Egg production by the Desert Tortoise (*Gopherus agassizii*) in California. Herpetologica 42:93–104.

Turner, F. B., K. H. Berry, D. C. Randall, and G. C. White. 1987. Population ecology of the Desert Tortoise at Goffs, California, 1983–1986. Report to Southern California Edison, Rosemead.

U.S. Fish and Wildlife Service. 1994. Desert Tortoise (Mojave Population) Recovery Plan. U.S. Fish and Wildlife Service, Portland, OR.

Wallis, I. R., B. T. Henen, and K. A. Nagy. 1999. Egg size and annual egg production by female Desert Tortoises (*Gopherus agassizii*): the importance of food abundance, body size, and date of egg shelling. Journal of Herpetology 33:394–408.

Wilbur, H. M., and P. J. Morin. 1988. Life history evolution in turtles. *In* C. Gans and R. B. Huey (eds.), Biology of Reptillia, pp. 387–439. John Wiley and Sons, New York.

Woodbury, A. M., and R. Hardy. 1948. Studies of the Desert Tortoise, *Gopherus agassizii*. Ecological Monographs 18:145–200.

Accepted: 6 August 2004.