VARIATION IN TORTOISE LIFE HISTORY: DEMOGRAPHY OF *GOPHERUS BERLANDIERI*

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Abstract. Turtles provide excellent models for studies of life history strategies, but terrestrial species are underrepresented in these analyses. We present a life table and demographic parameters of an inland population of *Gopherus berlandieri* to contribute to the study of evolution of turtle life histories. Data were gathered during a mark–recapture and radiotelemetry study in the Tamaulipan Biotic Province in southern Texas, USA. A total of 835 individuals were captured, measured, and their ages estimated. Females matured at 131 mm carapace length at an average of 5 yr of age (range: 4–8 yr). Clutch size, as determined by ultrasound, averaged 2.07 ± 0.15 eggs ($n = 49$). No nests were found, and we estimated clutch frequency with a quadratic model to be 1.34 clutches·female^{-1}·year^{-1}. Survival was estimated from age frequency regression and telemetry. Annual male survival (0.828, 0.834) differed ($P < 0.05$) from female survival (0.728, 0.774) for both techniques of estimation. Age-specific female survival ranged from 0.62 to 0.83 for 5- to 15-yr-old tortoises. Differential mortality of sexes led to a male-biased sex ratio in older age classes. Age structures of captured individuals did not vary ($P > 0.05$) among years, and population estimates did not differ among years; therefore, we constructed a life table under the assumption of a stationary population ($r = 0.0$). Under this assumption, survival from nest to age 4 yr must be at least 0.245, with hatchling survival of 0.528 to maintain a stationary population. *Gopherus berlandieri* matured at an earlier age, had smaller clutch sizes, and exhibited lower rates of female survival than other *Gopherus* species. We propose a physiological mechanism for lower female survival that implies trade-offs among egg size, subsequent hatchling survival, and female health. We maintain that high hatchling survival is necessary for population persistence. In an evolutionary context, we theorize that the selective advantages of small size and the life history strategies of *G. berlandieri* have been and are critical to its persistence.

Key words: demography; Gopherus berlandieri; life history; life table; sex ratio, age variation; species persistence; turtle.

INTRODUCTION

Life history theory examines the relationships between variation in life history traits and variation in individual fitness (Stearns 1989:14). Life histories are variously defined as a suite or set of demographic traits coevolved in response to ecological factors (Stearns 1976, Congdon and Gibbons 1990, Roff 1992). The testing of ecological and life history theory, and their application to conservation efforts, are hampered by the paucity of complete, species-specific data on life history traits in long-lived vertebrates (Congdon et al. 1994, Heppell 1998). Determination of age-specific survival and reproductive rates and their associated variation is necessary for rigorous tests of theory and the development of efficacious conservation programs. However, reliable data on intraspecific and interspecific variation in these characteristics are difficult to obtain.

Turtles have been identified as excellent models for the study of life histories of long-lived vertebrates

(Wilbur 1975, Congdon and Gibbons 1990). They occur at logistically reasonable densities, can be marked and monitored over long periods of time, and can be assessed for reproductive effort with noninvasive means (Wilbur 1975, Congdon and Gibbons 1990). The bulk of available life history data among the Testudines pertains to freshwater turtles, with long-term data sets available for *Chrysemys picta* (Wilbur 1975, Tinkle et al. 1981), *Trachemys scripta* (Frazer et al. 1990), *Kinosternon subrubrum* (Frazer et al. 1991), *K. flavescens* (Iverson 1991*b*), *Chelydra serpentina* (Congdon et al. 1994, Cunnington and Brooks 1996), and *Emydoidea blandingi* (Congdon et al. 1993). The life history strategy for turtles developed from these studies include high adult and juvenile survivorship, delayed sexual maturity, and low hatchling survival (Iverson 1991*b*, Shine and Iverson 1995). Life history variation in turtles comprises trade-offs between these factors and reproductive effort (Iverson 1992).

Demography of terrestrial turtles is less well understood and described. Populations of terrestrial species are more widely dispersed than aquatic species, thus they are more difficult to sample. Differences in de-
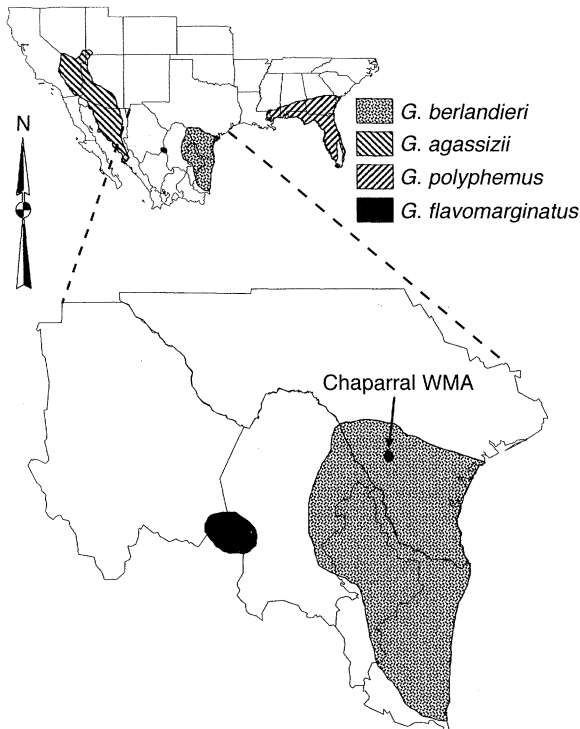
FIG. 1. Distribution of the four species of *Gopherus* in North America (top), and location of the Chaparral Wildlife Management Area, Dimmit and LaSalle Counties, Texas, USA, within the range of *G. berlandieri* (bottom).

mography between aquatic and terrestrial turtles may have implications for theory concerning evolution of turtle life histories. Analyses of available data suggest that terrestrial turtles exhibit higher hatchling survival (Iverson 1991a), larger eggs, and smaller clutches (Elgar and Heaphy 1989) than aquatic turtles. These patterns could reflect selection for larger eggs because of desiccation risk in terrestrial habitats, reduced mortality of large hatchlings because of size per se, or reduced predation pressure because of increased nest dispersion (Iverson 1991a). Morafka (1994) preferred that the large mass of neonatal *Gopherus* provided several adaptive advantages in variable terrestrial environments, such as greater strength, more physiological stability, and larger nutritional reserves.

The family Testudinidae, or tortoises, represents demographic extremes of iteroparity. In North America, four species of tortoises, all *Gopherus* spp., (Crumly 1994) are extant (Fig. 1). These tortoises are generally xeric- or arid-adapted species that function in some ecosystems (e.g., *G. polyphemus* in the southeastern United States) as keystone species (Bury and Germano 1994) because of their size and impacts on the environment. Although considerable work has been conducted on these species, demographic information is fragmentary (but see Turner et al. [1987] for a life table analysis of *G. agassizii*). A recent review of *Gopherus*

life history traits (Germano 1994b) pointed out gaps in our knowledge of the demography of these species. Data on survivorship, especially for the period from egg to 1 yr of age, and clutch frequency, are scant. Modeling of turtles (Congdon et al. 1993, 1994, Heppell 1998) and *G. agassizii* (Doak et al. 1994) showed that rates of population growth are most sensitive to changes in survival rates of adult females, underlining the importance of understanding these vital rates for conservation and management purposes.

The Texas tortoise (*G. berlandieri*) is the smallest but most sexually dimorphic of the four North American *Gopherus* (Rose and Judd 1982). Phylogenetically, it is most closely related to *G. agassizii* (Lamb et al. 1989, Lamb and Lydeard 1994, Morafka et al. 1994). Ecologically, it has been well studied in coastal environments (Auffenberg and Weaver 1969, Judd and Rose 1983, Bury and Smith 1986). However, life history traits are poorly described. Hatchling size (Auffenberg and Weaver 1969, Judd and McQueen 1980) and clutch size (Auffenberg and Weaver 1969, Judd and Rose 1989) have been documented, but clutch frequency is unknown. The only life stage for which survivorship data exist is that from egg to hatching (Germano 1994b), although individuals can live to more than 50 yr of age in captivity (Judd and McQueen 1982).

Our goal was to place *G. berlandieri* in the greater context of turtle and tortoise life history strategies. Germano (1994b) estimated that age at first reproduction was similar among the four *Gopherus*, and averaged 13.3 yr in *G. berlandieri*. If this is so, we predict that *G. berlandieri* should exhibit higher adult female survival, and/or have a higher clutch frequency than other North American *Gopherus*, to counter its small clutch size which averages 2.65 eggs (Judd and Rose 1989). This clutch size is smaller than in the larger *G. agassizzi*, reported at 4.5 eggs (Turner et al. 1986) and *G. polyphemus* with 5.2–8.9 eggs (Iverson 1980, Landers et al. 1980, Diemer and Moore 1994). An alternative trade-off, considering patterns of survivorship, growth, and age at sexual maturity among chelonians (Iverson 1991a, Shine and Iverson 1995), is that *G. berlandieri* matures at a younger age (see Auffenberg and Weaver 1969), and has lower female survival rates than other *Gopherus*. Decreasing the age at first reproduction can have powerful consequences on population growth rates in long-lived species (Cole 1954, Stearns 1989). To test these opposing predictions, our specific objectives were to determine age-specific reproductive and survival rates in an inland population of *G. berlandieri*, and to produce a life table from these vital rates. We also discuss implications of variability in life history strategies among *Gopherus* spp. in evolutionary and conservation contexts.

MATERIALS AND METHODS

Study area

We conducted research from April 1994 to August 1998 on the 6150-ha Chaparral Wildlife Management

Area (WMA) in Dimmit and LaSalle counties, Texas (Fig. 1). The Chaparral WMA has been managed as a research and demonstration area by the Texas Parks and Wildlife Department since its acquisition in 1969. It lies in the northern portion of the Tamaulipan Biotic Province (Blair 1950) and the western portion of the Rio Grande Plains ecoregion (Correl and Johnston 1979); and, therefore, is located near the northern edge of the distribution of the Texas tortoise. Rainfall is bimodally distributed with a major peak in May–June and a minor peak in September. Annual precipitation averages 66 cm (1969–1997; Texas Parks and Wildlife Department, *unpublished data*), but is highly variable and droughts are frequent (Norwine and Bingham 1986). The climate is characterized by hot summers (mean July temperature = 30.4°C) and mild winters (mean January temperature = 12.5°C). Freezes are rare and the length of the frost free period is typically 275–290 d (Hatch et al. 1990).

The vegetation of the area is dominated by honey mesquite (*Prosopis glandulosa*)–Acacia (*Acacia* spp.) thornscrub communities. Other communities, such as paloverde (*Parkinsonia texana*)- or ceniza (*Leucophyllum frutescens*)-dominated uplands or whitebrush (*Aloysia gratissima*)-dominated drainages, are locally significant. Common woody species include honey mesquite, blackbrush acacia (*A. rigidula*), guajillo (*A. berlandieri*), twisted acacia (*A. schaffneri*), granjeno (*Celtis pallida*), brasil (*Condalia hookeri*), and hog plum (*Colubrina texensis*). Prickly pear cactus (*Opuntia lindheimeri*) is abundant throughout the area. Dominant native grasses include hooded windmill grass (*Chloris cucullata*), fringed signalgrass (*Brachiaria ciliatissima*), hairy grama (*Bouteloua hirsuta*), and a variety of *Setaria* and *Paspalum*. Two introduced grasses, Lehmann lovegrass (*Eragrostis lehmanniana*) and buffelgrass (*Cenchrus ciliata*), are also abundant. Common forb species include croton (*Croton* spp.), crown coreopsis (*Coreopsis nuecensis*), partridge pea (*Chamaerista fasciculata*), crow poison (*Nothoscordum bivalve*), lazydaisies (*Aphanostephus* spp.), dayflower (*Commelina erecta*), verbenas (*Verbena* spp.), and plantains (*Plantago* spp.).

The Chaparral WMA was grazed by cattle before its purchase, and grazing continued until cessation in April 1984. Grazing resumed on 13 interior pastures from October to May in 1991 at a stocking rate of 6–28 animal-unit days/ha (1 animal-unit day equals grazing by 2 steers for 1 day). Two outlying pastures remained ungrazed since 1984.

Tortoise capture

Tortoises were captured by road cruising, intensive searches, and fortuitous encounters from 7 April 1994 to 12 August 1998, which encompassed five activity seasons. Data collected at each encounter included sex; straight-line carapace length (SCL; mm; dial calipers); mass (g; Pesola spring scale [Pesola AG, Barr, Swit-

zerland]); and age. Because adult female tortoises retain juvenile characteristics, a carapace length of 120 mm was used as the threshold length for determination of sex. Tortoises <120 mm SCL were considered juveniles, tortoises >120 mm SCL were considered adults. Among adults, tortoises with concave plastrons, thickened anal scutes, and enlarged chin glands (Rose and Judd 1982) were considered males. Adults without these characters were considered females. Earlier work has used 125 mm SCL as the threshold length for sexing (Judd and Rose 1983), but we found ~30 individuals of 120–125 mm SCL that had male characters, so we used 120 mm as the threshold in this population.

Population size, age structure, and sex ratio

We estimated population size of tortoises with the unbiased Petersen estimator (Krebs 1989, 1991) for 1994, 1995, and 1996. The estimate for any given year was based on tortoises initially marked in that year and the proportion of those tortoises recaptured during the following year by WMA personnel. Captured hatchlings were ignored to maintain demographic closure. Survival of marked and unmarked individuals was assumed to be equal. Immigration and emigration were assumed to be negligible because of the large study area (6150 ha) relative to the home range size of individual tortoises (<20 ha; R. T. Kazmaier, *unpublished data*). Confidence limits were based on the Poisson approximation for small samples (Krebs 1991).

We estimated the ages of tortoises by counting number of scute annuli (Germano 1988, Zug 1991, Germano and Bury 1998). Annuli were counted on 10 scutes by the same observer (RTK) and the mode was used to estimate age. Age refers to number of hibernations (i.e., winters); therefore, a 1-yr-old tortoise had one annulus. Tortoises without annuli were placed in a 0-yr age class. Annuli were discrete and countable on all tortoises examined on our study area. No tortoise had sufficient wear to the carapace or plastron to obscure annuli. Some tortoises on Chaparral WMA showed minor beveling at age 14, but beveling was minor even for the oldest individual (17 yr) examined. In contrast, tortoises examined by RTK in coastal areas of southern Texas exhibited pronounced scute beveling and wear.

Several recent studies have been critical of annuli techniques for estimating the age of turtles (Bjorndal et al. 1988, Brooks et al. 1997, Litzgus and Brooks 1998). Therefore, we compared ages at initial captures with ages at recapture in subsequent years (at intervals of 1–4 yr) to test the 1 annulus/yr hypothesis for this population. Ages of recaptured tortoises were estimated without knowledge of prior age estimates. Our recapture data indicated that Texas tortoises accumulate 1 annulus/yr and the scute annuli technique is a useful indicator of age in this population (Table 1).

A stable age structure occurs when the proportion of individuals in each class remains constant over time.

TABLE 1. Expected (assuming one annulus per year) and actual differences in the number of scute annuli of Texas tortoises based upon recaptures at Chaparral Wildlife Management Area, Dimmit and LaSalle Counties, Texas, from April 1994 to August 1998.

Expected annuli added (years between recaptures)	Actual annuli added ($\bar{X} \pm$ SE)	n	Proportion within 1 annulus of expected
1	0.99 ± 0.06	75	1.00
2	1.95 ± 0.09	40	0.95
3	3.07 ± 0.18	15	0.93
4	3.75 ± 0.25	4	1.00

To test for a stable age structure, we compared age frequency distributions of captured tortoises collected in each of 4 yr (1994–1997) with a χ^2 test of independence. Only 48 adults were aged in 1998 because of reduced effort, so these data were not included in age structure analyses. Each individual was counted only once. The first 100 individuals that were aged by scute annuli were deleted from this analysis to account for learning to interpret annuli for this population. Some of these individuals were subsequently recaptured and included in the analyses. Frequencies of tortoises in ages 4–12 (inclusive) were used in this analysis. At <4 yr of age, tortoises were greatly underrepresented in the capture sample (Table 2). At >12 yr of age, expected frequencies were <5 for every age because of small numbers of individuals captured. Sex ratio of adults overall and age-specific sex ratios were compared to a 50:50 sex ratio with Chi-square goodness-of-fit tests. We regressed sex ratio on age.

Reproduction

We estimated mean clutch size for the periods of May–July, 1996–1998, using an Aloka 500V portable ultrasound scanner (Corometric Medical Systems, Wallingford, Connecticut, USA) with a 7.5 linear convex transducer (Rostal et al. 1994). Orienting the probe in rear leg openings was sometimes difficult in *G. berlandieri* because of small body size, so x-ray analysis (Porta Ray MT Super 8020, St. Joseph, Missouri, USA. Settings: 15 MA, 70 KVP, 0.2 sec; Film: 3M Rare Earth System 400 green) was used on a subset of females to compare against ultrasound recordings. We averaged clutch size within age classes. However, because of small samples in each age class, we used an approach similar to that employed by Turner et al. (1987) to model age-specific clutch size for fecundity estimates in the life table analysis. Clutch size was regressed on carapace length. The distribution of carapace length in each year class was divided into quartiles. The midpoint of each quartile was entered into the clutch size-carapace length regression to provide a predicted clutch size for that quartile. Finally, the four predicted clutch sizes for each year class were averaged to provide a single, age-specific estimate for clutch size.

Intraseasonal clutch frequency is a difficult variable to measure in any turtle, and perhaps more difficult in terrestrial than aquatic turtles because of the dispersed nature of terrestrial individuals. We estimated mean clutch frequency by integrating a polynomial model developed from the temporal distribution of the proportion of gravid females in the population through the reproductive season. The model was of the form

$$P(x) = ax^2 + bx + c$$

where $P(x)$ is the probability of a female being gravid at a date x, where x is Julian date. Proportions of gravid females in semimonthly samples (e.g., 1–15 May) were used in the model. The parabolic shape of this model is justified by frequency diagrams of nesting dates in other turtles (Swingland and Coe 1978, Iverson and Smith 1993; but see Congdon et al. 1987). The integral of $P(x)$ gives the average number of days gravid per female during the nesting season, which we defined as 15 April to 19 July (Julian dates 105–200). These dates represent the beginning of the activity season and the latest observation of a female carrying shelled eggs (Judd and Rose 1989), respectively. We assumed that a female could retain eggs for an average of 30 days (Judd and Rose 1989). Therefore, dividing number of days gravid per female by 30 days per clutch provided an estimate of average clutch frequency for reproductively mature females.

Age-specific annual fecundity (female egg·female^{-1}·yr^{-1}) was estimated by multiplying the proportion of reproductively mature females by mean clutch size, by mean clutch frequency within a given year class, and by 0.5 (assuming an equal neonatal sex ratio). We used the minimal carapace length recorded for a gravid fe-

TABLE 2. Yearly age distribution of captured Texas tortoises at the Chaparral Wildlife Management Area, Dimmit and LaSalle Counties, Texas, from April 1994 to September 1997.

Age	1994	1995	1996	1997	Total
0	0	2	0	2	4
1	2	1	1	2	6
2	9	10	8	15	38
3	24	23	16	58	106
4	29	28	25	52	122
5	29	33	32	43	120
6	22	27	24	28	94
7	17	21	24	42	90
8	13	10	7	22	48
9	12	8	9	21	42
10	15	8	7	8	37
11	6	8	8	9	25
12	4	3	4	6	14
13	4	0	2	2	6
14	3	0	2	3	7
15	0	0	3	1	3
16	1	0	2	2	5
17	0	1	0	0	1

Note: Some rows do not add to "Total" because individuals recaptured in different years were counted only once for summation.

male and carapace measurements of females within each year class to estimate the age-specific proportion of reproductively mature females in each class.

Survivorship

We estimated survival rates for adult male and female tortoises by direct (radiotelemetered individuals) and indirect (standing age structure) methods. Radiotransmitters (~20 g, L. L. Electronics, Mahomet, Illinois, USA) were used on adults >600 g and mounted to the anterior portion of the carapace using silicon rubber. We relocated tortoises with transmitters using a 2-element, hand-held yagi antenna and a TR-4 receiver (Telonics, Mesa, Arizona, USA) at least once weekly during the active season (15 April–15 October), and once monthly during the inactive season (16 October–14 April). For telemetered tortoises ($n = 28$ females, 19 males), we estimated annual and interval survival rates for each sex using the Kaplan-Meier product limit method modified for staggered entry (Pollock et al. 1989). Staggered entry refers to the gradual addition of new individuals into the analysis as they are added to the radiomarked sample. We assumed that individual survival rates were independent, that individuals that were stagger entered had the same survival function as previously marked individuals, censoring was independent of animal fate (e.g., radio failure, emigration), and handling and marking did not affect survival probability. Annual survival rates were calculated for individual years from 1994 to 1997, and overall by converting all tortoise telemetry data to a single year. Differences in survival functions between sexes were compared with a log-rank test (Pollock et al. 1989). Age-specific survival rates for females also were estimated with the Kaplan-Meier method. Data from females that were monitored for >1 yr were included in >1 age class.

Annual survival for male and female tortoises also was calculated from age frequency data. We regressed log (frequency) on age for ages 5–11 (females) and 5–12 (males) with linear regression. The antilog of the slope of this line represented average annual survival for that age interval. Below 5 yr of age, animals were underrepresented in the capture sample presumably by virtue of cryptic behavior and limited movements. Numbers of captured individuals older than 11–12 yr of age were erratic and small. Survival estimated by this method integrated annual survival over several years. Sex comparisons for these estimates were made by testing regression lines for equal slopes with sex coded as a dummy variable.

We examined tortoise shells that we found for unusual wear and mortality signs. We compared the incidence (presence or absence) of perforations of the posteriormost costal bones by sex using a χ^2 test with Yates correction for continuity.

Life table analysis

After Congdon et al. (1993), we solved for hatchling survival in Euler's equation, $1 = \Sigma e^{-rx} l_x m_x$, while holding the exponential rate of increase (r) at zero. When $r = 0.0$, we had $1 = \Sigma l_x m_x$, where l_x was the product of annual survival rates through age class x, and m_x was the fecundity of a female of age x. This led to

$$1 = s_h m_1 + s_h s_a m_2 + s_h s_a^2 m_3 + \ldots + s_h s_a^{n-1} m_n$$

where s_h was hatchling survival (survival to 1 yr), and s_a was adult survival. We also assumed that juveniles (1–4 yr old) had survival rates equivalent to the average adult survival rate ($S_{female} = 0.774$; see Results, *Reproduction* section). Survival rates of juvenile desert tortoises (0.77–0.80) were of this magnitude (Turner et al. 1987, Heppell 1998). The above was solved algebraically to yield

$$s_h = 1/m_1 + s_a m_2 + \ldots + s_a^{n-1} m_n.$$

This was the hatchling survival rate that would give population stability at the specified values for s_a and m_x. Analyses were conducted through age 20.

RESULTS

Population size, age structure, and sex ratio

Number of captures/yr ranged from 144 to 316. Population estimates for 1994–1996 were 1576 (95% CL = 1061–2817), 1751 (1047–3324), and 1645 (1097–2702), respectively. Because of the underrepresentation of juvenile tortoises, these estimates represent an estimate of primarily adult tortoises that were vulnerable to capture by road cruising. Density estimates for the study area were 0.26–0.28/ha.

A total of 835 tortoises was captured 1020 times, with 284 juveniles (34.0%) and 551 adults (66.0%). After deleting the first 100 individuals and then including some of these individuals after being recaptured, 768 tortoises were used in subsequent analyses of age and sex. Age structures did not vary among years ($\chi^2 = 20.9$, 24 df, $P > 0.1$; Table 2). Therefore, we conducted further analysis on the pooled 1994–1997 sample ($N = 768$).

The sex ratio of the adult sample did not differ from 50:50 ($\chi^2 = 0.64$, 1 df, $P > 0.25$), with a total of 243 females and 261 males captured. However, based on regression, there was a change ($P = 0.004$) in sex ratio with age (Fig. 2). The sex ratio changed from female dominated at younger adult ages (4–6 yr old, with a female bias at age 6 [$\chi^2 = 3.88$, 1 df, $P < 0.05$]) to male dominated at older ages (7–15 yr old, with a male bias at age 12 [$\chi^2 = 4.57$, 1 df, $P < 0.05$]).

Reproduction

Average ($\pm$ 1 SE) clutch size of gravid tortoises assessed by ultrasound was 2.07 $\pm$ 0.15 eggs (range 1–4, $n = 49$). Age-specific clutch sizes varied little between ages 5 and 9, but appeared to increase at older ages
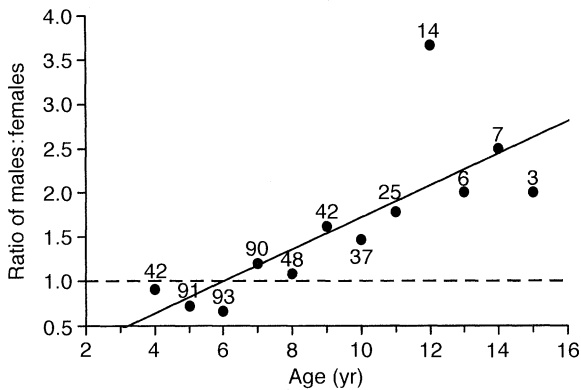
FIG. 2. Age-specific sex ratios of *G. berlandieri* captured on the Chaparral Wildlife Management Area, Dimmit and LaSalle Counties, Texas, USA, 1994–1997. Regression parameters for ages 4–15 yr were $Y = -0.08 + 0.18X$); df = 1, 10; $r^2 = 0.58$; $P = 0.004$. Numbers above symbols represent sample sizes.

(Table 3). For gravid tortoises that were examined by both techniques ($n = 14$), clutch size did not vary ($P > 0.05$) between x-ray (2.0 ± 0.3 eggs) and ultrasound (1.7 ± 0.4 eggs). In six cases, the egg count differed by one between techniques. In 30 additional cases, both techniques reported zero eggs. Ultrasound had a tendency to underestimate clutch size slightly because of eggs too anterior in the body cavity to detect or a leg opening too small for proper probe manipulation. Clutch size was weakly but significantly related to carapace length (clutch size = $-4.21 + 0.042$[carapace length]; $r^2 = 0.18$; 1,37 df; $P = 0.008$). The minimal carapace length recorded for a gravid female was 131 mm. This individual was 5 yr old. Females reached mature size between the ages of 4 and 8 yr (Table 4). By 7 yr of age, nearly all females (97%) exceeded this size.

The proportion of adult females identified as gravid by ultrasound was 0.35 ($n = 20$) in 1996, 0.37 ($n = 89$) in 1997, and 0.31 ($n = 35$) in 1998. Data were pooled across years (Fig. 3) to produce the predictive equation $P(x) = -3.12 + 5.0\cdot10^{-2} x - 1.70\cdot10^{-4}x^2$ ($r^2 = 0.97$). The integral of this equation between Julian dates 105 and 200, divided by 30 d (average number of days that a clutch is retained), yielded 1.34 clutches/female. Age-specific fecundity was calculated for ages ≥4 and provided input for the m_x column in the life table analysis.

Survivorship

Annual survival rates (S_x) were similar between estimation techniques. Based on Kaplan-Meier analysis, survival functions varied between sexes ($\chi^2 = 4.94$; $P = 0.026$), but endpoint annual survival rates did not differ ($S_{female} = 0.774$, 95% CI = 0.666–0.882; $S_{male} = 0.828$, 95% CI = 0.711–0.945; $P = 0.25$; Fig. 4). Based on linear regression of log-transformed age frequency distributions (Fig. 5), S_{female} (0.728 ± 0.023; $r^2 = 0.95$)

TABLE 3. Age-specific clutch sizes of Texas tortoises at Chaparral Wildlife Management Area, Dimmit and LaSalle Counties, Texas, from April 1994 to August 1998.

Age (yr)	n	Clutch size ($\bar{X} \pm$ SE)	Range
5	3	2.0 ± 1.0	1–4
6	9	1.7 ± 0.2	1–3
7	12	1.9 ± 0.2	1–3
8	9	2.0 ± 0.3	1–4
9	3	2.0 ± 0.0	
10	4	2.3 ± 0.8	1–4
11	7	2.9 ± 0.5	1–4
12	1	2.0	...
15	1	2.0	...

was lower ($P = 0.017$) than S_{male} (0.834 ± 0.029; $r^2 = 0.83$). Age-specific annual survival rates of adult females ranged from 0.62 to 0.83 (Table 5). We used these age-specific rates, rather than a single adult rate, in the life table analysis. Annual survival rates for adult females from 1994 to 1997 were 1.00, 0.82, 0.71, and 0.70, respectively.

No mortality among individuals carrying radiotransmitters occurred during the inactive period (15 October–14 April). The difference in survival functions between sexes appeared to be manifest in a wider temporal distribution of female mortalities. Male mortalities were concentrated in late summer (August and September). All mortality of tortoises with radiotransmitters ($n = 17$) appeared due to predation, but direct evidence of predation was usually lacking. Dead tortoises typically had the head and one or more legs removed. Nine of the recovered mortalities showed signs consistent with known raccoon (*Procyon lotor*) predation on sliders on our study area (R. T. Kazmaier, *personal observations*). A single raccoon hair was recovered from one of these mortalities. Five of the mortalities had damage consistent with being eaten by an avian predator with a raptorial beak. We tentatively

TABLE 4. Age-specific carapace length (mm) and body mass (g) of female Texas tortoises at Chaparral Wildlife Management Area, Dimmit and LaSalle Counties, Texas, from April 1994 to September 1997.

Age (yr)	Carapace length n	Carapace length $\bar{X} \pm$ SE	Body mass n	Body mass $\bar{X} \pm$ SE	Proportion exceeding 131 mm†
4	22	127.1 ± 1.3	30	495 ± 16	0.063
5	53	130.7 ± 0.9	71	555 ± 13	0.318
6	56	137.5 ± 1.0	67	619 ± 13	0.771
7	41	142.5 ± 1.0	50	689 ± 14	0.980
8	23	146.0 ± 1.8	32	742 ± 26	0.967
9	16	149.6 ± 2.6	30	756 ± 35	1.00
10	15	148.4 ± 2.3	19	803 ± 37	1.00
11	9	157.3 ± 2.6	17	826 ± 49	1.00
12	3	152.6 ± 2.0	6	880 ± 49	1.00
13	2	170.2 ± 19.0	5	993 ± 127	1.00
14	2	160.6 ± 4.2	4	798 ± 123	1.00
15	1	165.9		...	1.00

† Minimum size of a gravid female.

FIG. 3. Quadratic model [$P(x) = -3.12 + (5.0 \times 10^{-2})x - (1.70 \times 10^{-4})x^2$; $r^2 = 0.97$] of proportion of gravid *G. berlandieri* vs. time period on the Chaparral Wildlife Management Area, Dimmit and LaSalle Counties, Texas, USA, 1996–1998. Solid symbols indicate data from this study; open symbols indicate data from Judd and Rose (1989). Numbers represent sample sizes.
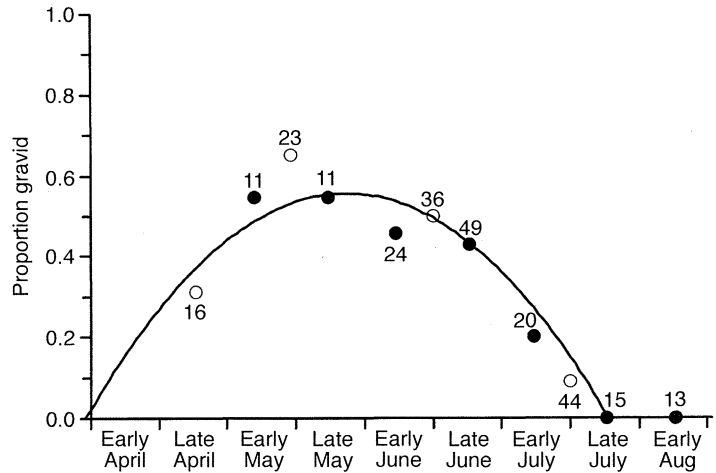
attributed these mortalities to crested caracaras (*Polyborus plancus*), based on four observations on CWMA of crested caracaras standing over live tortoises that had been flipped on their backs. The remaining three mortalities had inadequate evidence for speculation as to cause of death. We also cannot rule out the possibility that some of these tortoises died by other fates and were subsequently scavenged by mammalian or avian species.

Ninety tortoise shells found on the study area were examined for perforations of rear costal bones. We found that females ($n = 35$) were more likely ($\chi^2 = 21.0$, 1 df, $P < 0.001$) than males ($n = 55$) to have perforations resulting from wear from the pelvic girdle.

Life table analysis

We could not estimate survivorship of nests, hatchlings, or juveniles (1–4 yr old). In four full seasons of field monitoring 15–20 radiomarked females, we were unable to locate a single nest. Also, as is apparent from the age structure of the capture sample (Table 2), young

tortoises were underrepresented. Therefore, we cannot present a complete life table. However, we used the results presented for reproduction and adult survivorship to estimate survival rates of hatchling tortoises necessary to maintain a stationary population (see Materials and Methods, *Life table analysis* section), which was suggested by our population estimates and evidence of a stable age structure (similar age distributions among yearly capture samples). We used the following data to construct the life table: female maturity at 131 mm, clutch frequency of 1.34/yr, age-specific clutch size based on the carapace length-clutch size regression and the distribution of carapace lengths within each age class (Table 4), and age-specific survival of females ≥ 4 yr old (Table 5). Life history parameters of adult female tortoises in our population necessitated 24.5% survivorship of hatchling tortoises to 4 yr of age (Table 6) to maintain a stationary ($r = 0.0$) population. If we increased the female sex ratio at hatching to 0.524 (the observed sex ratio at age 4), necessary survivorship to age 4 to maintain a stationary population decreased to
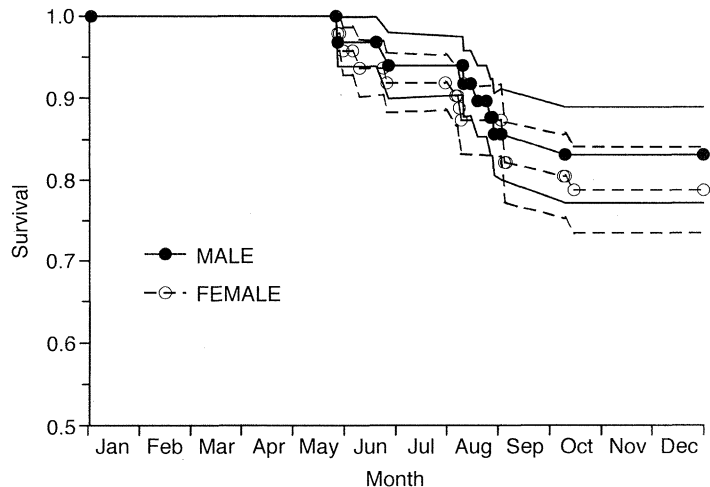

FIG. 4. Kaplan-Meier estimates of annual survival for 19 male and 28 female *G. berlandieri* radio-marked on the Chaparral Wildlife Management Area, Dimmit and LaSalle Counties, Texas, USA, 1994–1997. Solid and dashed lines without symbols represent ± 1 SE.
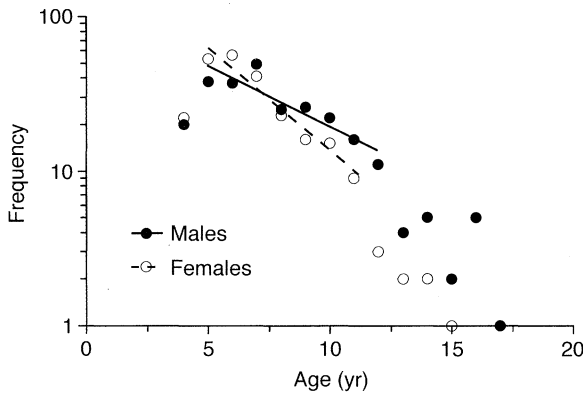
FIG. 5. Regression of log-transformed frequency distributions on age for female [log $(Y) = 2.501 - 0.138X$; $r^2 = 0.95$; $P < 0.001$] and male [log $(Y) = 2.074 - 0.079X$; $r^2 = 0.83$; $P = 0.002$] G. berlandieri captured on the Chaparral Wildlife Management Area, Dimmit and LaSalle Counties, Texas, USA, 1994–1997. Slopes ($P = 0.017$) and intercepts ($P < 0.001$) of regressions were different. Regressions were restricted to tortoises in the 5–12-yr range.

23.4%. Assuming annual juvenile survival is 0.774 (the same as adult females), then survival from egg laying to 1 yr of age must reach 0.528. The life table also explains the lack of older tortoises in our sample. Given our survival estimates, only five of 1000 hatchling tortoises would survive to age 20.

DISCUSSION

Life history strategies and evolution of turtles have been discussed by several authors (Wilbur and Morin

TABLE 5. Age-specific, annual survival rates (S) of adult female Texas tortoises using the Kaplan-Meier product-limit method (Pollock et al. 1989) on the Chaparral Wildlife Management Area, Dimmit-LaSalle counties, Texas, from 20 June 1994 to 1 September 1997.

Age (yr)	n	Total radiodays†	$S \pm$ SE
5–7	16	3243	0.825 ± 0.100
8	11	2827	0.762 ± 0.124
9	13	2963	0.619 ± 0.156
10	9	2132	0.729 ± 0.170
11	8	1862	0.833 ± 0.152
12–15	17	5020	0.820 ± 0.110

† Number of days that tortoises of this age group were monitored, where one tortoise monitored for one day constitutes one radioday.

1988, Congdon and Gibbons 1990, Shine and Iverson 1995). Demography of G. berlandieri contributes new data to our knowledge of turtle life histories. Like other turtles, G. berlandieri exhibits iteroparity. However, the suite of life history characteristics in G. berlandieri suggest that it is less K selected relative to other Gopherus, or is less of a bet-hedging strategist, depending on a deterministic or stochastic view of demography (Stearns 1976).

Age at maturity and adult female survival

Gopherus berlandieri matured at an earlier age and exhibited lower rates of female survival than other Gopherus. Modeling of turtle populations has shown that changing the age at maturity has less impact on r than other parameters have, notably adult female survival

TABLE 6. Life table for Gopherus berlandieri at the Chaparral Wildlife Management Area in southern Texas based on demographic parameters reported in text, and varying the intraseasonal clutch frequency.

Age	Clutch frequency = 1.1/yr			Clutch frequency = 1.34/yr			Clutch frequency = 1.9/yr		
	l_x	m_x	$l_x m_x$	l_x	m_x	$l_x m_x$	l_x	m_x	$l_x m_x$
0	1.000	0.0		1.000	0.0		1.000	0.0	
1	0.643	0.0		0.528	0.0		0.372	0.0	
2	0.498	0.0		0.408	0.0		0.288	0.0	
3	0.385	0.0		0.316	0.0		0.223	0.0	
4	0.298	0.041	0.012	0.245	0.050	0.012	0.173	0.071	0.012
5	0.246	0.229	0.056	0.202	0.279	0.056	0.142	0.396	0.056
6	0.203	0.657	0.133	0.167	0.800	0.133	0.117	1.134	0.133
7	0.167	0.940	0.157	0.137	1.145	0.157	0.097	1.623	0.157
8	0.138	1.003	0.139	0.113	1.222	0.139	0.080	1.733	0.139
9	0.105	1.114	0.117	0.086	1.357	0.117	0.061	1.925	0.117
10	0.065	1.099	0.072	0.053	1.339	0.072	0.038	1.899	0.072
11	0.047	1.249	0.059	0.039	1.522	0.059	0.027	2.157	0.059
12	0.040	1.280	0.051	0.032	1.559	0.051	0.023	2.210	0.051
13	0.032	1.472	0.048	0.027	1.793	0.048	0.019	2.543	0.048
14	0.027	1.472	0.039	0.022	1.793	0.039	0.015	2.543	0.039
15	0.022	1.472	0.032	0.018	1.793	0.032	0.012	2.543	0.032
16	0.018	1.472	0.026	0.015	1.793	0.026	0.010	2.543	0.026
17	0.014	1.472	0.020	0.011	1.793	0.020	0.008	2.543	0.020
18	0.011	1.472	0.016	0.009	1.793	0.016	0.006	2.543	0.016
19	0.008	1.472	0.012	0.007	1.793	0.012	0.005	2.543	0.012
20	0.006	1.472	0.009	0.005	1.793	0.009	0.004	2.543	0.009

Notes: The study population was estimated at a clutch frequency of 1.34/yr. The first four l_x values assume maintenance of a stationary population of tortoises. Life tables for 1.1 and 1.9 clutches per year are also presented; these bracket estimates for G. agassizii (Turner et al. 1986).

(Iverson 1991*a,* Congdon et al. 1993). However, Cole's (1954) discussion illustrated that the sensitivity of *r* to age at maturity is much greater when this age is small. Therefore, the disparate age at maturity in *G. berlandieri* compared to other *Gopherus* has dramatic demographic consequences.

Age at maturity in other *Gopherus* ranges from 9 to 21 yr in *G. polyphemus* (Iverson 1980, Landers et al. 1982, Diemer and Moore 1994, Mushinsky et al. 1994), with an approximate mean of 15, and from 13 to 16 yr in *G. agassizii* (Turner et al.1987, Germano 1994*b*). Previous estimates of age at first reproduction for *G. berlandieri* were divergent, ranging from 3–5 yr in Auffenberg and Weaver (1969) to 13.3 yr in Germano (1994*a*). The higher estimate was based on growth curves from scute rings, which may have underestimated carapace growth, and a minimum size of females with eggs of 155 mm (Rose and Judd 1982). Subsequent work in coastal *G. berlandieri* found a gravid female of 142 mm (Judd and Rose 1989), a size reached in our tortoises as early as 6 yr of age.

We calculated growth rates (mm/yr) of recaptured juvenile tortoises to verify that tortoises could grow fast enough to reach mature size in this time span. We estimated growth rates by dividing the difference in SCL between captures by time for tortoises <120 mm SCL at their initial capture. Recaptures were excluded from analysis if they occurred <9 mo from the initial capture. Mean growth rate of juvenile tortoises (15.9 ± 0.7 mm/yr, *n* = 52) supported the concept of rapid attainment of size at maturity. Carapace length at hatching in *G. berlandieri* is 40 mm (Judd and McQueen 1980). We conclude that modal age at first reproduction in the inland population of tortoises that we studied is 5 yr, based on average carapace length at this age and increasing sexual dimorphism in body size after age 6 (R. T. Kazmaier, *unpublished data*).

Shifts in adult survival rates are associated with concurrent shifts in age at maturity in turtles (Shine and Iverson 1995), a point well demonstrated by *G. berlandieri.* Our data on adult female survival and age at maturity sit squarely in the center of data for these variables among turtles (Shine and Iverson 1995:Fig. 2). Annual survival of adult females of *G. agassizii* is generally >0.90 (Turner et al. 1984, 1987), but can be lower during extended drought (Peterson 1994). Survival rates of adult *G. berlandieri* were slightly lower than those of immature subadult *G. agassizii,* reported at ~0.84 by Turner et al. (1987). These turtles are similar in size (100–179 mm) to *G. berlandieri* (Doak et al. 1994). Demographically, early age at maturity allows *G. berlandieri* to trade off moderate levels of female mortality and maintain population persistence despite low fecundity.

Sex ratio

Several demographic factors can influence the adult sex ratio within a population (Gibbons 1990, Lovich

and Gibbons 1990). In our study population, the shift in sex ratio toward male dominated, older age classes is a mathematical consequence of higher male survival. A secondary influence may be reduced vulnerability of females to capture, as evidenced by the lower estimate for female survival based on age frequency regression compared to Kaplan-Meier analysis. At early ages, females predominated, perhaps as a consequence of an earlier age at maturity (Lovich and Gibbons 1990). Three of four other studies of *G. berlandieri* have reported capturing more (*P* < 0.05) adult males than females (Gibbons 1990). We propose that higher female mortality is associated with the smaller size of females at maturity, rendering them more vulnerable to predation and physiological costs of reproduction.

We offer the following physiological hypothesis for higher mortality in females, based on our observations of a higher incidence among females of perforations in the rear part of the carapace. We propose that calcium deficiency is produced in female Texas tortoises by an interaction of the calcium cost of producing large eggs, a diet seasonally high in *Opuntia* fruit and cladodes (R. T. Kazmaier, *unpublished data*), and thin bony shells designed to expand for egg development and egg laying (Rose and Judd 1991). Female *G. agassizii* maintain high concentrations of serum calcium during vitellogenesis and egg shell deposition (O'Connor et al. 1994, Rostal et al. 1994; C. C. Peterson, Oklahoma State University, *unpublished data*), presumably to provide the calcium for these processes.

Physiological and behavioral evidence suggests that dietary calcium is inadequate to meet the calcium demands of egg development. During egg development, elevated concentrations of serum phosphate (O'Connor et al. 1994), a minimal component of the calcium carbonate-dominated egg shell but a large proportion of the hydroxyapatite matrix of bone, is evidence that bone is resorbed to provide the necessary calcium. Several species of tortoises are known to consume bones, stones, and soil (Esque and Peters 1994). We also found *G. berlandieri* exhibiting geophagy during direct observations and radiography. Twenty-eight of 45 x-rayed female tortoises contained some calcium source (soil, stones, snail shells) in their digestive tract. Mineral supplementation is usually postulated as the purpose of this behavior, and most geophagy by *G. agassizii* is on calcium-rich substrates by adult females (Marlow and Tollestrup 1982, Esque and Peters 1994). Consumption of *Opuntia* may exacerbate a shortage of dietary calcium. It is high in calcium oxalates (Theimer and Batemen 1992), which reduce calcium availability. Therefore, consumption of *Opuntia* may intensify bone resorption to produce eggs. Over time, calcium deficiency could lead to thinner shells until the pelvic girdle breaks through the carapace. The already thin shells of *G. berlandieri* (Rose and Judd 1991) may render this species uniquely susceptible to this deficiency. High female mortality may result from increased suscepti-

bility to pathogens, impaired movement, or directly from calcium deficiency. Coupled physiological and demographic data are needed to test this hypothesis.

Data from other turtle species suggest that systematic differences in adult survival rates between sexes are rare (Gibbons 1990). One exception occurs in a population of *Testudo hermanni* in which mean annual survival in males (S_{male} = 0.91) was slightly higher than in females (0.88) and the population was male biased. The difference was proposed to result from increased female mortality from wounds following courtship (Hailey 1990). In other studies, gender differences in survival rates were not statistically significant. For *G. agassizii*, male and female survival were similar in one study area (Turner et al. 1984), and male survival (S_{male} = 0.91) was slightly lower than female survival (0.94) in another area (Turner et al. 1987). In the Kinosternidae and Emydidae, male and female survival rates are essentially identical (Frazer et al. 1991, Iverson 1991*a*), slightly higher in females (Wilbur 1975, Mitchell 1988), or slightly higher in males (Frazer et al. 1990).

Reproduction

Clutch size is smaller in *G. berlandieri* than in other *Gopherus*, not surprising considering the positive relationship between clutch and body size in turtles in general (Iverson 1992) and testudinids in particular (Elgar and Heaphy 1989). Previous estimates of clutch size bracketed our estimates, from 1.65 (Auffenberg and Weaver 1969) to 2.65 (Judd and Rose 1989) and 4.3 eggs (Rose and Judd 1982). Judd and Rose (1989) failed to find a significant relationship between clutch size and carapace length, although they noted that clutches of 5 eggs were observed only in females >180 mm in carapace length, and that females <155 mm in carapace length did not produce a clutch of >3 eggs. Mean clutch sizes of populations of the other three species of *Gopherus* vary from 4 to 8 eggs (Germano 1994*b*), with intraspecific variation associated with body size observed in *G. polyphemus* (Diemer and Moore 1994).

Clutch size is probably maximized given egg and body size constraints in *G. berlandieri*. We found a 5-yr-old individual of 133.5 mm that contained four eggs. A radiograph of this individual suggested that additional eggs in the body cavity might impair digestive function. Food intake and gut fill is decreased in gravid desert tortoises (Meienberger et al. 1993). Egg size and pelvic aperture are not correlated to female body size in *G. berlandieri* (Judd and Rose 1989, Long and Rose 1989), suggesting that morphological constraints do not limit egg size in this species (Congdon and Gibbons 1987). Variation in egg size is less than variation in clutch size (Judd and Rose 1989), and thus consistent with optimal egg size theory (Congdon and Gibbons 1987). Adaptations in *G. berlandieri* for large egg size include larger pelvic apertures in females (Long and

Rose 1989), loose skeletal connections in the pelvic area, and a plastral hinge to facilitate laying of large eggs (Rose and Judd 1991). The potential physiological costs of these adaptations (thin carapaces, large eggs) in decreasing adult female survival (see Discussion, *Sex ratio* section) are presumably a trade-off for increased hatchling survival.

Reviews have reported that terrestrial turtles lay larger eggs in smaller clutches than aquatic turtles (Wilbur and Morin 1988, Elgar and Heaphy 1989), but exhibit higher early age class survival (Iverson 1991*a*). Life history traits of *G. berlandieri* are consistent with this scenario. It may be most informative to compare demographic traits of the tortoise with similar-sized aquatic turtles, such as *Chrysemys picta* (Wilbur 1975, Tinkle et al. 1981) and *Trachemys scripta* (Frazer et al. 1990). Females in the studied populations of these emydids reached maturity at 7 yr and exhibited adult survival rates of 0.76–0.82 annually. These values are close to those of our study population. However, clutch sizes of the aquatic turtles were 6–7.5 eggs, 3-fold higher than the terrestrial *G. berlandieri*. The tortoise trades off smaller clutch size with higher annual recruitment (see Discussion, *Recruitment* section).

Clutch frequency has a dominant influence on annual variation in reproductive output in turtles (Gibbons 1982). In *G. berlandieri*, Judd and Rose (1989) could not identify double-clutching in 29 females that were radiographed multiple times, although other observations suggest that it may occur in the species (Auffenberg and Weaver 1969, Judd and Rose 1989). Our modeling of clutch frequency based on changing proportions of gravid females provided evidence that some females lay two clutches in a single season. If egg retention is shorter than we assumed (30 d), such as in desert tortoises (22.3 d: Turner et al. 1986), the clutch frequency estimate would be higher. Number of clutches/yr in other *Gopherus* range from 1.0 in *G. polyphemus* (Iverson 1980, Landers et al. 1980) to 1.1–1.9 in *G. agassizii* (Turner et al. 1984, 1986). In terrestrial species with long nesting seasons and where individuals are sampled only once during this season, we believe that our model is a useful first pass at estimating clutch frequency. Other models, e.g., a bimodal form or a skewed distribution with an extended right tail, may be more appropriate for other species.

We suspect that we may be underestimating clutch frequency in *G. berlandieri*. Iverson (1992) reported an inverse relationship between age at maturity and clutch frequency in turtles, which he attributed to constraints imposed by small body size in early maturing turtles. In areas with long growing seasons, production of multiple clutches offsets the constraint of optimal egg size on clutch size (Moll 1979, Congdon and Gibbons 1985, Hailey and Loumbourdis 1988), allowing greater and more successful reproductive effort than a single clutch of either a few large eggs or many small eggs. European tortoises (*Testudo graeca, T. hermanni,*

and T. marginata) produce 2–3 clutches/yr (Swingland and Stubbs 1985, Hailey and Loumbourdis 1988, Diaz-Paniagua et al. 1996). Using an equation relating annual relative clutch mass to age at maturity in turtles (Iverson 1992: Fig. 4) for *G. berlandieri,* and assuming a clutch size of 2.0, average egg mass of 26.9 g (Judd and Rose 1989), adult mass of 800 g, and age at maturity of 5 yr, yields an estimated clutch frequency of 4.0/yr.

Recruitment

The only critical demographic variable for which we have no data is juvenile survival, or survivorship from hatching to 4 yr of age. Neonatal life history remains a missing link in most turtle life history analyses (Morafka 1994). Given the other life history traits exhibited by *G. berlandieri,* this species must trade off small clutch sizes and moderate rates of adult female survival with moderate hatchling (52.8%) and juvenile survival (24.5% from hatch to age 4) to maintain stationary or produce growing populations. Comparatively, juvenile *G. agassizii* (<100 mm) had estimated annual survival rates from life table analysis of 0.77–0.80 (Turner et al. 1987), identical to our assumed rates. Annual survival of 32 *G. polyphemus* juveniles (1–4 yr old) was 0.45 (Wilson 1991).

Evidence for moderate to high nest and hatchling survival in testudinids is equivocal, but accumulating. Most early reports suggested high nest predation and hatchling mortality in *Gopherus* (Alford 1980, Landers et al. 1980) and other turtles (Wilbur and Morin 1988). However, with the advent of miniaturized telemeters and thread-trailing methods, direct estimates of hatchling survival have been made. Butler and Sowell (1996) monitored two cohorts of *G. polyphemus* hatchlings. Annual survival rates of these cohorts were 0.53 (*n* = 14, radiomarked) and 0.0 (*n* = 17, but only six were followed to death). Unpublished data mentioned by Adest et al. (1989) for *G. flavomarginatus* in Mexico suggested annual hatchling survival of 0.33. Turner et al. (1987) estimated egg-laying to yr-1 survival to be 0.47 in a population of *G. agassizii.* These estimates are lower than that required for our population to remain stationary. However, if clutch frequency in *G. berlandieri* is actually 1.9 clutches/yr, as observed for *G. agassizii* (Turner et al. 1986), then survival of 0.37 from egg-laying to 1 yr of age meets the condition of $r = 0.0$, if other parameters are held constant (Table 6). These survival values are possible.

Recent data from *Testudo graeca,* which has several similarities in life history and ecology with *G. berlandieri,* provide provocative evidence that survival from the nest to 1 yr of age is in the range necessary to maintain a population. In a Spanish population, hatching success was 82.4% and hatchling survival was 0.39, indicating 32% survival from egg laying through the first winter (Diaz-Paniagua et al. 1997, Keller et al. 1998). Nest predation was absent in a Greek population

of *T. hermanni,* a related species (Swingland and Stubbs 1985). These two European populations and inland *G. berlandieri* in southern Texas share a nest-dispersal strategy that may reduce nest predation and increase recruitment. In other *Gopherus,* nests are laid at the entrance to a burrow, a behavior that may facilitate location of nests by predators (Diaz-Paniagua et al. 1997). In *G. berlandieri* (Auffenberg and Weaver 1969) and *Testudo graeca* (Diaz-Paniagua et al. 1996), eggs are not laid in specific nesting areas, but are dispersed in small, cryptic nests. Clutch partitioning among separate nests also can occur (Judd and Rose 1989). Finally, adult female *G. berlandieri* carrying radiotransmitters commonly made extensive forays out of their resident home range during the nesting season (R. T. Kazmaier, *unpublished data*), similar to *T. graeca* (Diaz-Paniagua et al. 1996). Although we did not locate nests, we suspect that these movements, which occurred only during the nesting season, were part of a nest-dispersal strategy.

Evolutionary considerations

The bet-hedging model predicts that a fluctuating environment that causes wide variation in juvenile mortality will lead to delayed maturity, decreased annual reproductive effort, and longer lived individuals. Conversely, if environmental variation affects adult survival more strongly, the resultant life history tactic is predicted to be early maturity, shorter life, and greater reproductive effort (Stearns 1976). On the continuum of tortoise life histories, *G. berlandieri* tends toward the latter pattern. Morafka (1994) believed that *G. berlandieri* would have stable recruitment relative to the two desert *Gopherus* because of consistently high rainfall and availability of continuous habitats. We concur, although we note that *G. berlandieri* inhabits the environment with the most variable precipitation (based on constancy and contingency of rainfall) of all *Gopherus* (Norwine and Bingham 1986, Germano 1994a). Nevertheless, annual precipitation rarely drops below 30 cm in a drought year, and thus exceeds amounts in rainy years in the Mojave, Sonoran, and Chihuahuan habitats of *G. agassizii* and *G. flavomarginatus* (Germano 1994a). Interannual variability in clutch frequency and recruitment remain major needs in data sets for *G. berlandieri,* other *Gopherus,* and other turtles to test these ideas. Variation in body size (Bury and Smith 1986) and density (Judd and Rose 1983) between moist coastal and semiarid inland populations hint at environmental influences on demographics. We agree with Frazer et al. (1991) on the importance of studies to document life history variability within and between species.

Why does *G. berlandieri* have a life history strategy disparate from other extant *Gopherus*? We develop a brief scenario based on the historical biogeography and evolution of the genus (Bramble 1982, Morafka 1988). Nine to 23 species of *Gopherus* occurred in the fossil

record of North America from the early Oligocene to the Pleistocene (Auffenberg and Franz 1978a, Bramble 1982, Crumly 1994). Only four species remain, the systematics of which remain contentious. However, the mtDNA phylogeny presented by Lamb and Lydeard (1994) identified *Gopherus* spp. as a monophyletic group of two clades (*G. agassizii–G. berlandieri* and *G. polyphemus–G. flavomarginatus*). Human predation has been proposed as the primary cause of a massive range contraction of *G. flavomarginatus,* and by extension, broad extinctions in the *Gopherus* and *Geochelone* assemblages, in the late Pleistocene (Morafka 1988). Morafka (1988) speculated that the extensive burrow systems of *G. flavomarginatus* and *G. polyphemus* accounted for survival of these species. *Gopherus agassizii* also builds burrows and survives in harsh environments. However, *G. berlandieri* rarely builds or uses burrows (Auffenberg and Weaver 1969, Rose and Judd 1982).

We theorize that the life history strategy of *G. berlandieri* is central to its persistence. Morafka (1988) noted that shell lengths of some *Gopherus* lineages have been greatly reduced since the late Pleistocene. Human predation during the Pleistocene, which was typically on larger species and individuals (McDonald 1984), may have selected for smaller, early maturing individuals. Early maturation would have permitted *G. berlandieri* to withstand relatively high rates of female mortality. Alternatively or in combination, nutritional limitation and climate changes may have been responsible for dwarfing in the late Pleistocene (Guthrie 1984). A third possibility is that *G. berlandieri* was already small and cryptic at the time of the human invasion in the Pleistocene, thereby reducing its importance as prey. Historically and presently, a diverse mesopredator complex (raccoon, *Procyon lotor*; coyote, *Canis latrans*; bobcat, *Felis rufus*; crested caracara, *Polyborus plancus*; and possibly others) likely exerted continual selective pressure on *G. berlandieri* to retain characteristics of early maturity and small, well concealed clutches. The lack of a fossil record (Auffenberg and Franz 1978b) makes it impossible to separate these possibilities. In any case, *G. berlandieri* and its sister taxa *G. agassizii* have evolved different life history characteristics.

We conclude with a few remarks on turtle conservation. A recent paper on life history theory, population modeling, and turtle conservation posed the following question: "Is it best to test possible management scenarios for poorly known Berlandier's tortoises (*Gopherus berlandieri*) on a model population of congeneric gopher tortoises (*Gopherus polyphemus*) or yellow mud turtles (*Kinosternon flavescens*), which have a similar age at maturity, clutch size, and lifespan (Heppell 1998: 367)" We answer yes to the second option. Although Morafka et al. (1994) stated that extrapolations from one species of *Gopherus* to another are warranted when conservation decisions are needed quickly

and life history characteristics for the taxon of interest are not available, our study highlights problems with this approach as we have expanded the range of life history strategies attributable to *Gopherus*. The inland population of *G. berlandieri* that we studied had lower adult female survivorship, smaller clutch sizes, and an earlier age to maturity than any other extant *Gopherus*. Indeed, these parameters also were different from those of *K. flavescens* (Iverson 1991b). Nevertheless, we agree strongly with Heppell (1998) that population models and conservation scenarios should be applied to species with similar life history characteristics rather than based simply on phylogeny. For example, Van Buskirk and Crowder (1994) proposed that similarities in life histories among marine turtles were conducive to model extrapolation across species.

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