Herpetological Monographs, 32, 2018, 34–50
© 2018 by The Herpetologists' League, Inc.

Reproductive Ecology and Life History of Female Sonoran Desert Tortoises (*Gopherus morafkai*)

Roy C. Averill-Murray[1,3,6], Terry E. Christopher[2,4], and Brian T. Henen[2,5]

[6] Nongame Branch, Arizona Game and Fish Department, 5000 West Carefree Highway, Phoenix, AZ 85086, USA
[2] Smithsonian Institution, Department of Zoological Research, National Zoological Park, 3001 Connecticut Avenue, Washington, DC 20008, USA

Abstract: We studied female *Gopherus morafkai* reproduction for 10 yr to evaluate reproductive variation and environmental factors that influenced reproduction. In contrast to vitellogenesis in other *Gopherus*, substantial follicle growth occurred during the spring after emergence from hibernation. Vitellogenesis and egg production varied considerably among individuals. The smallest egg-producing female had a carapace length of 220 mm, and no female produced more than one clutch per year. Compared to small females, large females were more likely to reproduce in a given year and produced larger eggs, but body size did not affect clutch size. Good maternal body condition contributed to follicle growth in winter, larger clutches, and larger eggs in a clutch. Females that emerged from hibernation earlier were more likely to produce eggs. Early-emerging females also produced larger eggs than did females that emerged later. These reproductive traits contribute to a life history that resembles an income breeder compared to the more capital-breeding strategy of the closely related Mojave Desert Tortoise (*Gopherus agassizii*). These life history differences might convey different reproductive and population consequences of climate change.

Key words: Egg production; *Gopherus agassizii*; Mojave Desert Tortoises; Reproduction; Reptilia; Testudines; Testudinidae; Ultrasonography; Vitellogenesis; X-ray radiography

Variation in reproductive cycles within and among climates illustrates the remarkable flexibility in how chelonians time reproduction to improve the survival of parent and offspring (Congdon et al. 1982; Turner et al. 1986; Hofmeyr 2004; Averill-Murray et al. 2014). This flexibility has enabled chelonians to persist through climate changes over geological time (Kuchling 1999). The long-lived, iteroparous nature of chelonians (Congdon et al. 1982), plus their marked physiological tolerances (e.g., Nagy and Medica 1986; Henen 1997; Henen et al. 1998; Jackson 2011), support flexible reproductive responses to variations in weather and enable them to hedge their reproductive bets. The bet-hedging strategy might manifest as few but large clutches in species with predictable reproductive seasons or in many reproductive bouts for species living in highly variable and unpredictable environments (Congdon et al. 1982; Iverson 1992; Henen 1997). The latter case, where resources are unpredictable, might increase the likelihood of recruitment coinciding with favorable conditions.

For example, North American testudinids (*Gopherus* spp.) that inhabit more predictable environments (*Gopherus morafkai* and *G. polyphemus*) reproduce less frequently, but at a larger maternal size, than those species inhabiting less predictable environments (*G. agassizii* and *G. berlandieri*; Averill-Murray et al. 2014). Gopher Tortoises (*G. polyphemus*) experience the greatest amount of annual precipitation and reliable forage among the species, and females produce a maximum of one, albeit large, clutch each year. In contrast, Mojave Desert Tortoises (*G. agassizii*) inhabit the most seasonal and least productive environment; they produce up to three clutches per year and the greatest, size-specific annual fecundity among *Gopherus* species (Averill-Murray et al. 2014).

In addition to shaping chelonian life histories, environmental factors also cue reproduction by triggering physiological processes or by synchronizing circannual rhythms with the time of year (Kuchling 1999; Hofmeyr 2004). In Painted Turtles (*Chrysemys picta*), warm temperatures inhibit follicular growth, while cooler temperatures stimulate vitellogenesis (Ganzhorn and Licht 1983). High temperatures initially stimulate ovarian growth in Eastern Musk Turtles (*Sternotherus odoratus*) and Indian Flapshell Turtles (*Lissemys punctata*), but after extended exposure to high temperatures, females resorb their follicles (i.e., the follicles become atretic; Mendonça 1987; Sarkar et al. 1996). Egg-maturation rate in Green Sea Turtles (*Chelonia mydas*) increases with seasonal increases in water temperatures (Weber et al. 2011), and warm temperatures facilitate oviposition in Tent Tortoises (*Psammobates tentorius*; Leuteritz and Hofmeyr 2007).

We lack studies of environmental effects on reproductive physiology of *Gopherus*, but ultrasound scanning over multiple years can help us better understand the underlying gonadal mechanisms that affect egg production under different environmental conditions (Rostal et al. 1994; Kuchling 1999; Henen and Hofmeyr 2003). In *Gopherus*, vitellogenesis occurs mostly in the fall prior to hibernation, when follicles are nearly fully developed and consistent in size, and is completed in spring shortly before or after emerging from hibernation (see review by Rostal 2014). For example, ovarian follicles in *G. agassizii* mature to near-ovulatory size (2.3-cm diameter) by October and achieve a maximum size of 2.4 cm after emerging from hibernation (Rostal et al. 1994). Nevertheless, studies of reproduction in North American tortoises have employed primarily X-ray radiography (X-ray) to measure clutch size, clutch frequency, and egg size (recently reviewed by Averill-Murray et al. 2014). Factors affecting the female reproductive cycle and

[3] Present address: Desert Tortoise Recovery Office, US Fish and Wildlife Service, 1340 Financial Boulevard, #234, Reno, NV 89502, USA
[4] Present address: Great Basin Institute, 16750 Mount Rose Highway, Reno, NV 89511, USA
[5] Present address: Environmental Affairs Division, Marine Air Ground Task Force Training Command, Marine Corps Air Ground Combat Center, Twentynine Palms, CA 92278, USA
[6] Correspondence: e-mail, roy_averill-murray@fws.gov

reproductive output in Sonoran Desert Tortoises (*G. morafkai*) have been studied relatively little compared to that of other *Gopherus* spp. (Averill-Murray et al. 2014; Rostal 2014).

With 4 yr of X-rays, Averill-Murray (2002a) showed that *G. morafkai* produced a maximum of one clutch of eggs each year, with winter and spring rainfall influencing whether females produced eggs but not influencing clutch size. Sexual differences in winter behavior (e.g., greater winter activity by females; Bailey et al. 1995; Sullivan et al. 2014) indicate that proximate environmental factors might also influence reproduction in Sonoran Desert Tortoises. Long-term studies are critical to understand the complexities of *Gopherus* reproductive ecology, within and among species (e.g., Congdon and Gibbons 1990; Congdon et al. 2003). Consequently, we added 6 yr of X-ray data and 5 yr of ultrasound data in the same population of Averill-Murray (2002a), plus 3 yr of ultrasound data from a second population, to describe annual and individual variation in *G. morafkai* reproduction. We used seasonal rainfall and temperatures, body condition, and timing of emergence from hibernation to investigate environmental factors that might influence ovarian cycles (follicle size and growth) and egg production (clutch frequency, clutch size, and egg size). We also interpret how the reproductive patterns contribute to the life history of Sonoran Desert Tortoises and contrast that against the life history of the closely related Mojave Desert Tortoise.

Materials and Methods

Study Area and Seasons

We studied adult female *G. morafkai* in the northeastern Sonoran Desert near Sugarloaf Mountain on the Tonto National Forest, Maricopa County, Arizona, USA, using the methods described by Averill-Murray (2002a). The study area contained vegetation classified in the paloverde–mixed cacti series of the Arizona Upland Subdivision of the Sonoran Desert (Turner and Brown 1982). Arroyos divided a rolling topography of steep, rocky slopes with boulders up to 4 m in diameter. With the exception of one tortoise (no. 14) who moved about 2.5 km in September 1998, the study occurred over 260 ha, with elevations from 549 to 853 m. A state highway delineated the eastern boundary of the study area, and recreational target shooters heavily used the southernmost boundary. An active livestock grazing allotment encompassed the study area, but we rarely observed evidence of cattle on the site.

We recorded rainfall each week from a rain gauge located on a hill (elevation ca. 707 m) in the western portion of the study area. We summarized seasonal rainfall each year according to periods defined by average environmental conditions and tortoise activity (Averill-Murray et al. 2002; Table 1). Summer (July–October) included the monsoon (rainy) season and peak tortoise activity. Winter (November–February) was usually wet, but cool and with little tortoise activity. Early spring (March–April) generally included increasing tortoise activity, while late spring (May–June) included ovulation and nesting, which extended into summer. We estimated long-term weather norms from 1940 to 1992 data at the nearest National Oceanic and Atmospheric Administration weather station (Stewart Mountain, ca. 13 km to the south, 433 m elevation). We also indicated when seasonal rainfall at Sugarloaf (recorded weekly from a rain gauge) deviated more than two standard deviations from long-term norms for Stewart Mountain (Table 1).

We used daily Stewart Mountain maximum and minimum temperatures to calculate daily mean temperatures from 1 January 1992 through 31 July 2005, although there were occasional (5%) gaps in the data. We deployed an Optic Stowaway temperature data logger (Onset Computer Corporation) within the canopy of a creosote bush next to the rain gauge from July 1996 to October 2003. The data logger recorded shaded air temperatures hourly, from which we calculated daily mean, maximum, and minimum temperatures, but data logger records covered 48% of the study duration. To correct the broader Stewart Mountain dataset for the local Sugarloaf climate, we regressed maximum and minimum temperatures (within each of three 4-mo seasons: winter, spring, summer) for Stewart Mountain against the data logger data. Minimum and maximum temperatures were correlated between sites. When data logger temperatures were not available, we estimated them using the relevant regression equation to the Stewart Mountain (StM) data:

$$\text{Winter}_{\text{min}} = \text{StM} \times 0.72 + 1.23 (n = 603; R^2 = 0.57),$$

$$\text{Winter}_{\text{max}} = \text{StM} \times 1.07 + 0.77 (n = 603; R^2 = 0.63),$$

$$\text{Spring}_{\text{min}} = \text{StM} \times 0.97 + 0.37 (n = 842; R^2 = 0.85),$$

$$\text{Spring}_{\text{max}} = \text{StM} \times 1.09 + 2.80 (n = 842; R^2 = 0.79),$$

$$\text{Summer}_{\text{min}} = \text{StM} \times 0.78 + 4.99 (n = 875; R^2 = 0.69), \text{or}$$

$$\text{Summer}_{\text{max}} = \text{StM} \times 1.05 + 4.71 (n = 872; R^2 = 0.66).$$

We estimated the mean daily temperature by averaging the daily minimum and maximum values.

Telemetry and Radiography

We used telemetry (Averill-Murray 2002a) to monitor female tortoises (184–289 mm midline carapace length [CL]) weekly year-round in 1993 and from 1997 through 2005 (Appendix). We estimated the date that each tortoise terminated hibernation as the last day the tortoise was observed inside or <10 m from its hibernaculum. We used the YearFrac function in Microsoft Excel to convert this date to the fraction of the calendar year transpired. Three individuals emerged in December, so we subtracted 1 from their YearFrac to indicate emergence during the calendar year preceding the reproductive season.

We began X-ray radiography (or ultrasonography; see below) on 12 June 1993, 15 May 1997, and, in all other years, early to mid-April after females emerged from hibernation, using methods described by Averill-Murray (2002a). We generally began regular, biweekly radiographic sampling during May. In 1993, palpation indicated that we missed radiographic data from one clutch laid prior to 12 June. We did not radiograph a tortoise if palpation confirmed it was

Table 1.—Seasonal and annual rainfall (mm) at Sugarloaf Mountain, Arizona, prior to the summer reproductive season. Summer = July to October prior to year of reproduction (Year − 1); winter = November to February; early spring = March to April; late spring = May to June. Sugarloaf values deviating by >2 SD from long-term means at Stewart Mountain (1940 to 1992) are indicated with arrows (based on square root–transformed data), indicating significantly above- or below-average periods (↑ or ↓, respectively).

Year	Summer (Year − 1)	Winter	Early spring	Late spring	Total
1993	221.2	367.0↑	90.5	2.1	680.8↑
1997	68.6	76.5	44.0	6.5	195.6
1998	83.3	252.4	74.1	0.0	409.8
1999	96.1	72.1	61.2	0.0	229.4
2000	128.6	10.4↓	83.1	24.9	247.0
2001	201.6	118.6	79.2	2.5	401.9
2002	30.9	57.6	9.1	0.0	97.6↓
2003	80.3	100.3	115.6	0.0	296.2
2004	94.4	90.9	113.1	0.0	298.4
2005	151.5	357.0↑	35.5	0.0	544.0
Mean (SD)	115.7 (60.10)	150.3 (127.74)	70.5 (33.80)	3.6 (7.77)	340.1 (173.40)
1940–1992	128.5 (63.50)	131.3 (74.64)	49.3 (40.55)	9.9 (13.23)	347.6 (123.67)

still gravid; this minimized handling, radiographic exposure, and stress to individuals (Hinton et al. 1997; Kuchling 1998). Ultrasonography (below) also obviated unnecessary radiography to tortoises that had not ovulated. Beginning in 1998, we provided drinking water to tortoises that voided their bladders during processing to further minimize handling effects (Averill-Murray 2002b). Then we returned tortoises to their capture locations.

Beginning in 1999, we processed small tortoises (below 220 mm CL) every third week instead of second week to limit handling and radiation exposure; eggs were not detected in tortoises below 220 mm in two populations (Averill-Murray 2002a). We report summary statistics for these subadult tortoises, but exclude them from all statistical tests.

We counted clutch size directly from radiographs, measured egg width to 0.05 mm with calipers, and corrected for magnification (Gibbons and Green 1979; Graham and Petokas 1989). For this correction, we used 30 mm as the egg-to-film distance (Wallis et al. 1999). We used an individual's last egg-bearing radiograph of a season to measure egg widths when multiple images were taken in a season.

Ultrasonography

We used ultrasonography similar to that described by Rostal et al. (1994) and Henen and Hofmeyr (2003) to monitor ovarian and oviductal status on four to six occasions annually from 1999 to 2003. We scanned females inguinally using an Aloka 500-V portable ultrasound scanner (Corometrics Medical Systems), with a 7.5-MHz convex linear transducer, at intervals of 5 to 8 wk during the active season. We held females upright, extended their hind limbs manually, and applied Aquasonic Ultrasound Gel (Parker Laboratories) as a coupling gel. The probe was oriented medially and craniomedially to view the ovaries and oviducts. We used the scanner's digital calipers to measure the diameter (±0.1 cm) of vitellogenic follicles and egg yolks from the left and right inguinal views. We used follicle diameter to estimate follicle volume (a sphere), summing them to calculate total follicle volume in each tortoise. When eggs were present but not all visible in the ultrasound scan (see Henen and Hofmeyr 2003), we estimated total yolk volume by multiplying clutch size by the yolk volume averaged from visible yolks. We similarly sampled 21 females (1 to 7 observations/female) from 2001 to 2003 near Saguaro National Park, Pima County, Arizona. We investigated potential differences in vitellogenesis depending on reproductive status during the current reproductive season (Repro), as well as during the previous season (PreRepro). We excluded inconclusive tortoises for which data gaps prevented determination of reproductive condition.

Statistical Analysis

Vitellogenesis.—We investigated summer vitellogenesis between oviposition and hibernation by subtracting the first estimate of follicle volume following oviposition from the last estimate before hibernation within individual females. We used mixed models with nlme (Pinheiro et al. 2016) in R v3.3.2 (R Core Team 2016) to assess variables potentially affecting vitellogenesis. Models included combinations of the fixed effects PreRepro, body condition index (BCI = mass [g] divided by carapace length [cm]; Wallis et al. 1999) following oviposition, and their interaction. We included individual tortoise as a random effect. We standardized continuous input variables (e.g., z.CL = standardized CL) and centered binary input variables (e.g., c.PreRepro = centered PreRepro) using the MuMIn package (Barton 2014), which allows direct comparison of relative variable importance in reducing variance within models (Schielzeth 2010). Visual assessment of residuals and variances led us to apply a varIdent variance structure on PreRepro to correct for heteroscedasticity (Zuur et al. 2009).

As for summer, we calculated winter vitellogenesis by subtracting the last estimate of follicle volume before hibernation from the first estimate in spring for each female. Fixed effects included combinations of Repro, BCI, and their interaction; individual tortoise was a random effect. Visual assessment of residuals and variances led us to drop one outlier, which improved model fit and homogeneity of variances. Similarly, we subtracted the first estimate of follicle volume in spring from the first estimate of yolk volume for each gravid female to compute spring follicle/yolk growth. For females forgoing egg production, we subtracted spring follicle volume from the estimated follicle volume on the sample date when most reproductive females contained shelled eggs. Fixed effects included Repro, BCI, and their interaction; individual tortoise was a random effect.

Through these and subsequent analyses, we used MuMIn and bias-corrected Akaike information criteria (AIC_c) to identify the top model set as that including all models with a relative likelihood ≥ 0.05 ($\Delta AIC_c \leq 6$; Burnham and Anderson 2002:171; Arnold 2010). If necessary, we computed model-averaged, maximum-likelihood parameter estimates and unconditional variances (multi-collinearity was minimal, with $|r| < 0.25$ among model-averaged variables; Cade 2015). We excluded models from the candidate set if they were more complex versions of models having a lower AIC_c value, and we did not average models containing an interaction term (Burnham and Anderson 2002; Richards et al. 2011). Where model averaging was not necessary, we recomputed the final model with restricted maximum likelihood to improve variance estimates (Zuur et al. 2009). We calculated marginal and conditional R^2 ($R^2_{[m]}$ and $R^2_{[c]}$, respectively; Nakagawa and Schielzeth 2013) for the global models with piecewiseSEM (Lefcheck 2015). We report 85% confidence intervals (CIs), rather than 95% CI, to make model-selection and parameter-evaluation criteria congruent (Arnold 2010).

Reproductive output.—Given the greater number of years available for clutch frequency, clutch size, and egg size compared to the vitellogenesis samples, we applied a sequential process to evaluate models of random and fixed effects (Zuur et al. 2007). No tortoise laid more than one clutch in a year, so relative clutch frequency equaled the probability of reproducing in a year. First, we used the R package lme4 (Bates et al. 2015) to search for the optimal set of random effects among both tortoise identification number and year with the fixed effect of standardized carapace length. We also included standardized clutch size as a fixed effect in the egg size analysis. We selected the optimum random-effect structure as that with the lowest AIC_c. We used generalized linear mixed models for the probability of reproducing (logit link and binomial error distribution) and clutch size (log link and Poisson error distribution), and we used linear mixed models for egg size. We excluded clutch frequency data from 2005 due to the high proportion of females of inconclusive reproductive status.

Second, we used the base model to assess the effects of rainfall and air temperature on the response variable using the R package climwin (van de Pol et al. 2016). We assessed linear and logarithmic effects of weekly rainfall summed over windows ranging from 0 to 38 wk preceding 23 July, the latest date clutches were first detected on radiographs. The maximum window (38 wk; i.e., as far back as 30 October of the prior year) allowed consideration of potential effects of winter and spring precipitation on vegetation growth for forage, and the logarithmic analysis incorporated a possible asymptotic relationship. We also assessed linear effects of daily mean air temperature averaged over the same window (266 d). We used the randwin function and the P_C statistic in climwin to assess the likelihood that the climate signal in the best model was obtained by chance by running 10 randomizations of the best model. However, large eigenvalue ratios caused the randomized models to fail in the clutch frequency analysis, so we evaluated whether the best model was spurious simply by calculating the proportion of all models that occurred in the 95% confidence set; a real climate signal is more likely if the models within the 95% confidence set comprise a small percentage of the total models tested (Bailey and van de Pol 2016).

Finally, we applied a hierarchical approach for three additional variables because data were available for only a subset of cases for each variable. We compared the final model from the climate analysis with a model that included the additional variable after restandardizing the reduced input data (Arnold 2010). First, we added emergence date (z.YearFrac) to determine whether timing of hibernation emergence influenced reproductive output. For clutch frequency, we dropped two outliers to improve model fit and proceeded with multi-model selection, as above. Next, we repeated the process by adding c.PreRepro to assess the effect of reproduction in the prior year on reproductive output during the current year, using the subset of data for which we had prior-year information. Then, we added z.BCI to assess the effect of female body condition. In the clutch frequency and clutch size analyses, random effects had zero variance so we used generalized linear models with the stats package in R.

Results

Rainfall

Annual and seasonal rainfall varied greatly among years, with coefficients of variation ranging from 48% to 216% (Table 1). The wettest year, 1993, received >136 mm more rain than the next wettest year and was almost double the long-term mean; it had the wettest summer (172% of long-term mean), wettest winter (280%), and third wettest early spring (184%). The driest year, 2002, had below-average rainfall in every season and only 28% of the long-term annual mean. The winter of 2000 was especially dry with only 10.4 mm (8%). With the exception of 2000, late spring received little to no rain.

Emergence from Hibernation

The average date of emergence from hibernation was 8 March and ranged from 22 January for reproductive females in 2003 to 22 April for nonreproductive females in 2000 (YearFrac = 0.06 and 0.30, respectively; Table 2). Individuals emerged as early as 7 December (2002) and as late as 24 June (1999). Emergence dates of subadults broadly overlapped those of adult females in every year except 2002 and 2003, when subadults tended to end hibernation later than adults (Table 2).

Vitellogenesis

The seasonal volume of ovarian follicles varied from year to year. Following the summer egg-laying season, follicle volume was low (<20 cm^3), with follicles absent in 49% of all postoviposition and prehibernation samples (Fig. 1A,B). Follicle volumes increased by the first spring measures, with 22% of all records exceeding 20 cm^3 (Fig. 1C). When females were gravid, yolk volumes ranged from 17.3 to 91.2 cm^3 (clutch size = 2 to 9), and nonreproductive females had <40 cm^3 of follicles (Fig. 1D). Compared to other years, follicle volume in the driest year (2002) was low before the reproductive season ($\bar{X} = 3.0$ cm^3, $n = 8$), and no follicles were observed following the reproductive season ($n = 12$). Three of the four sampled females that produced eggs in 2002 lacked detectable follicles in spring. The pattern of

TABLE 2.—Spring emergence (YEARFRAC mean ± 1 SD) by female Sonoran Desert Tortoises at Sugarloaf Mountain, Arizona. YEARFRAC is the fraction of the calendar year at which hibernation terminated. Samples sizes are listed in the header rows. Calendar dates for the mean are indicated. Ranges are given in parentheses. Subadult carapace length <220 mm.

	1997	1998	1999	2000	2001	2002	2003	2004	2005
Egg layers	3	10	6	9	9	5	6	8	6
	0.18 ± 0.00	0.18 ± 0.045	0.18 ± 0.050	0.17 ± 0.080	0.19 ± 0.033	0.17 ± 0.043	0.06 ± 0.064	0.16 ± 0.028	0.11 ± 0.038
	8 March	8 March	8 March	5 March	12 March	5 March	22 January	27 February	11 February
	(0.18)	(0.13–0.29)	(0.13–0.22)	(−0.01 to 0.24)	(0.09–0.24)	(0.10–0.20)	(−0.03 to 0.14)	(0.12–0.19)	(0.07–0.17)
Non–egg layers	5	4	8	7	6	5	2	0	0
	0.21 ± 0.082	0.22 ± 0.065	0.26 ± 0.111	0.30 ± 0.106	0.21 ± 0.021	0.16 ± 0.126	0.10 ± 0.027	—	—
	19 March	21 March	7 April	22 April	19 March	27 February	8 February		
	(0.12–0.31)	(0.15–0.29)	(0.15–0.48)	(0.18–0.45)	(0.18–0.24)	(−0.07 to 0.25)	(0.08–0.12)		
Subadults	2	3	2	2	3	3	3	3	0
	0.19 ± 0.027	0.22 ± 0.062	0.23 ± 0.110	0.22 ± 0.027	0.18 ± 0.019	0.31 ± 0.127	0.19 ± 0.031	0.18 ± 0.011	—
	12 March	21 March	25 March	21 March	8 March	24 April	12 March	8 March	
	(0.18–0.21)	(0.17–0.29)	(0.15–0.30)	(0.22–0.26)	(0.16–0.20)	(0.18–0.43)	(0.16–0.22)	(0.17–0.19)	

follicle development near Saguaro National Park matched that at Sugarloaf (Fig. 1).

In summer following oviposition, the volume of ovarian follicles decreased by a mean of 0.4 cm^3 (SD = 6.02, range = –28.0 to 11.2 cm^3). The varIdent structure in the global model indicated that vitellogenesis in females that did not reproduce in the previous season was over twice as variable as in females that reproduced the previous season ($SD_{PreRepro,no\ eggs}$ = 2.68, $SD_{PreRepro,eggs}$ = 1.00 [2.79:1.00 in the final model, below]). All models were within 6 AIC_c units of each other, but all models containing fixed effects had less support than the intercept-only model, which indicated that follicles did not grow during summer (85% CI = –0.6 to 1.4 cm^3, $R^2_{[m]} = 0$, $R^2_{[c]} = 0.10$, $n = 43$).

Over winter, mean volume of ovarian follicles increased 9.8 cm^3 (SD = 14.68, range = –6.4 to 62.6 cm^3). The top model included the body-condition fixed effect, and all other models within 6 AIC_c units were eliminated as more complex. Females starting the reproductive cycle (i.e., entering hibernation) in better condition experienced greater follicle growth over winter than those in poorer condition ($\hat{\beta}_{z.BCI} = 5.5$, 85% CI = 2.8 to 8.1, $R^2_{[m]} = 0.21$, $R^2_{[c]} = 0.21$, $n = 37$; Fig. 2).

In spring, ovarian follicles grew 36.0 cm^3 (SD = 19.16, range = 2.6 to 81.0 cm^3) in reproductive females (becoming yolks) and 7.5 cm^3 (SD = 16.10, range = –22.5 to 34.8 cm^3) in nonreproductive females. Correspondingly, the top model for spring follicle growth included only the fixed effect of reproductive status ($R^2_{[m]} = 0.39$, $R^2_{[c]} = 0.47$, $n = 29$); all other models within 6 AIC_c units were eliminated as more complex. The predicted increase in volume from follicles to yolks in reproductive females was 28.9 cm^3 (85% CI = 18.2 to 39.5 cm^3), and predicted increase in follicle volume in nonreproductive females was 4.2 cm^3 (85% CI = –0.8 to 9.2 cm^3).

Females vitellogenic in spring commonly failed to produce eggs. Eleven females (55%) with follicles >2 cm diameter, and 12 of 25 (48%) females with 1- to 2-cm follicles did not produce eggs in the ensuing season. Of 18 ultrasound observations on adults containing at least one near-ovulatory follicle (diameter >2 cm during the preovulation or ovulation periods), nine (50%) females failed to produce shelled eggs that season (two in 1999, two in 2000, two in 2002, and three in 2003). Winter rainfall was below average every year during our ultrasound sampling. However, rainfall in winter 2001 was 90% of average and was preceded by a wet summer (157% of average; Table 1). Still, mature follicles (>2-cm diameter) were rare in early spring, during which only one of 12 ultrasound scans detected a mature follicle, but this and five other tortoises developed eggs after beginning with relatively small (<2 cm) follicles.

Of 26 females that produced eggs and had ultrasound data in the same season, nine (35%) had mature follicles (>2-cm diameter; 21 to 49 d between detection of mature follicles and detection of shelled eggs), and nine (35%) had intermediate-sized follicles (1 to 2 cm; 16 to 56 d). One female had only small follicles (<1-cm diameter, 35 d), and seven (27%) had no detectable follicles or only atretic follicles (21 to 43 d) during the spring prior to ovulation. The greatest disparity in follicle development between preovulatory and gravid stages occurred in the driest year, 2002. Of females with follicles <2 cm in diameter in early spring,

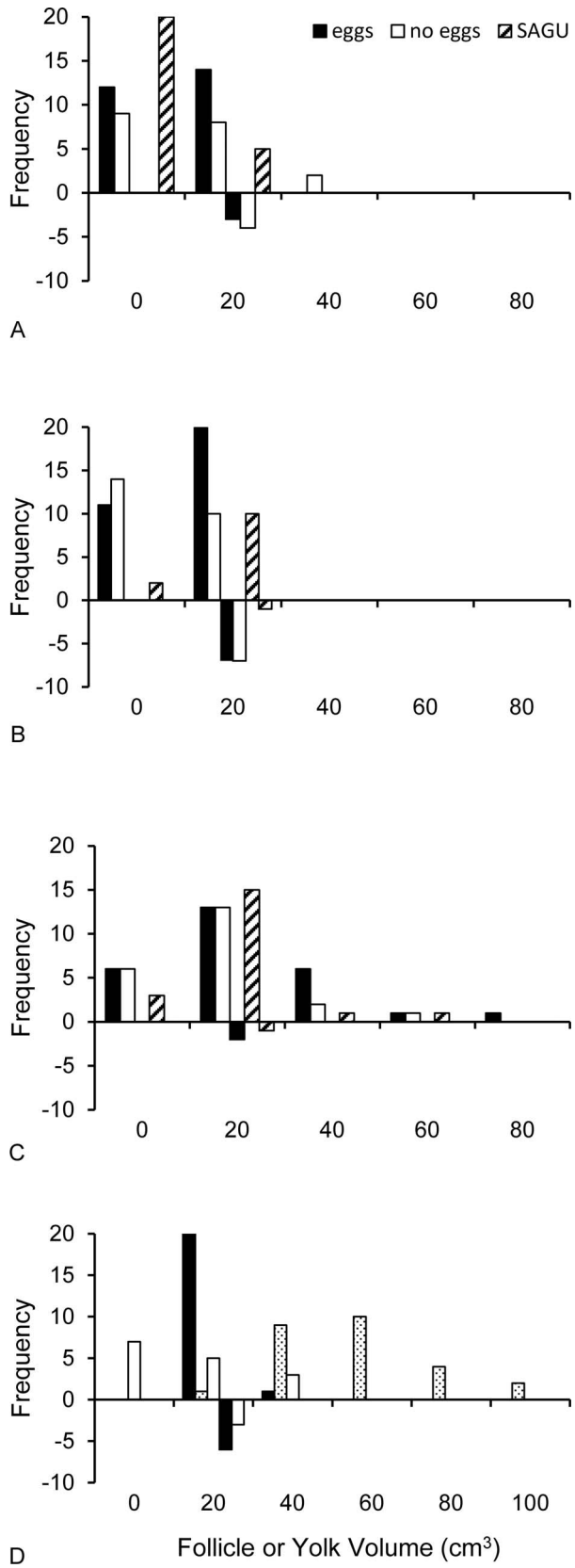

FIG. 1.—Volume of vitellogenic follicles and yolks in Sonoran Desert Tortoises at Sugarloaf Mountain, Arizona, from 1999 to 2003, and near Saguaro National Park (SAGU), Arizona, from 2001 to 2003. Panels indicate ultrasound scan data immediately following oviposition in summer/autumn (A = postovulation), before hibernation in autumn (B = prehibernation), before ovulation in spring (C = preovulation), and during the period when most females were gravid in late spring (D = ovulation). Bars represent females that produced eggs (black) and females that did not produce eggs (white) in the upcoming reproductive season at Sugarloaf Mountain; stippling indicates yolk volumes. Females at SAGU (hatched bars) were not recaptured consistently during each stage and are not divided by reproductive condition. Negative values indicate volume of atretic follicles.

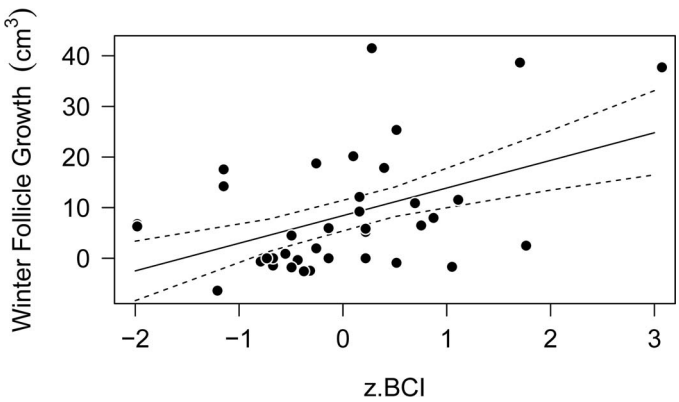

FIG. 2.—Ovarian follicle growth over winter, with 85% confidence limits, relative to standardized body condition index (z.BCI) of Sonoran Desert Tortoises at Sugarloaf Mountain, Arizona. $R^2_{(m)} = 0.21$, $R^2_{(c)} = 0.21$. Unstandardized sample mean BCI = 0.17 (±0.02 SD).

those that ovulated tended to be slightly more active in March and April than were females that did not ovulate (6.8 ± 1.38 unique locations [n =17] and 5.9 ± 1.79 [n = 14], respectively; $t_{29} = -1.7$; $P = 0.10$), despite having similar volumes of follicles ($\bar{X}$ = 10.0 ± 13.3 cm^3 and 8.9 ± 11.5, respectively; $t_{29} = -0.2$; $P = 0.82$).

We detected ovarian follicles in tortoises <220 mm CL on only three of 47 scans of six individuals. The smallest female with follicles had CL of 186 to 194 mm from 1999 to 2000 and had only small follicles: one 0.6-cm follicle in May 1999 and two follicles (0.6 and 0.7 cm) in April 2000. Despite this female growing to 213 mm in 2004, we never detected follicles in 10 subsequent scans or eggs in two radiographs in 2004. The next largest female (no. 616, CL = 217 mm) had four vitellogenic follicles (0.9 to 1.5 cm) and one atretic follicle (0.8 cm) in September 2001.

Reproductive Output

Clutch frequency.—Annual clutch frequency ranged from 0.36 to 1.00 (Table 3). The climate analysis resulted in 94% of 35,778 temperature windows within the 95% confidence set, precluding predictive value of temperature on the probability of reproducing. The probability of reproducing was greater for larger females ($\hat{\beta}_{z.CL} = 0.70 \pm 0.357$ SE, $P = 0.049$, $n = 116$). The best rainfall model differed from the top temperature model by $AIC_c = 0.71$ and indicated a linear effect of rainfall during the week of 9 April ($\hat{\beta}_{rainfall} = 0.23$, SE = 0.072, Z = 3.23, $P = 0.001$). This also was a spurious effect, though, with 93% of the 780 rainfall windows occurring within the 95% confidence set.

We retained body size in the emergence-date analysis, and the model with emergence date outperformed the model with only body size by $\Delta AIC_c = 23.77$ ($R^2 = 0.28$, $n = 91$). The probability of reproducing was inversely related to emergence date ($\hat{\beta}_{z.YearFrac} = -1.78$, 85% CI = –2.58 to –1.13), with body size positively affecting reproductive probability by

TABLE 3.—Mean (± 1 SD) size and reproductive characteristics of female Sonoran Desert Tortoises at Sugarloaf Mountain, Arizona. CL = carapace length. Ranges are given in parentheses. Subadult CL <220 mm.

	1993	1997	1998	1999	2000	2001	2002	2003	2004	2005
Sample size[a]	10	11	18[b]	16	18[b]	15	10[b]	9	10[b]	6[b]
Egg layers	8	4	12	7	10	9	5	6	10	6
CL (mm)	247 ± 12.9 (220–260)	253 ± 11.5 (239–288)	249 ± 16.4 (229–287)	260 ± 16.8 (239–289)	253 ± 12.9 (230–273)	261 ± 13.3 (246–288)	248 ± 12.5 (230–263)	258 ± 11.3 (228–275)	253 ± 17.7 (230–287)	253 ± 16.1 (230–275)
Clutch frequency[e]	0.80 ± 0.13	0.36 ± 0.15	0.68 ± 0.11	0.44 ± 0.13	0.56 ± 0.12	0.60 ± 0.13	0.50 ± 0.17	0.67 ± 0.17	1.00 ± 0.00	—[c]
Clutch size[e]	5.7 ± 2.43 (3–9)[d]	3.8 ± 1.26 (2–5)	5.4 ± 1.16 (4–7)	4.6 ± 1.51 (3–7)	5.5 ± 1.72 (3–9)	5.3 ± 1.66 (3–9)	5.0 ± 1.22 (3–6)	4.8 ± 1.79 (2–6)[d]	5.8 ± 2.17 (3–9)[d]	5.0 ± 1.41 (3–7)
Egg width (mm)[e]	35.7 ± 1.74 (32.1–37.7)[d]	35.0 ± 1.23 (33.6–36.6)	35.4 ± 1.73 (33.0–39.7)	36.3 ± 2.15 (33.8–39.8)	36.2 ± 1.21 (34.2–38.1)	36.2 ± 1.46 (33.1–37.8)	36.4 ± 1.20 (34.8–38.0)	36.5 ± 1.02 (35.1–37.8)[d]	36.3 ± 0.88 (34.6–37.5)[d]	37.1 ± 0.50 (36.4–37.6)
Non-layers	2	7	5	9	8	6	5	3	0	0
CL (mm)	235 ± 20.5 (220–249)	246 ± 20.7 (221–288)	242 ± 9.2 (233–254)	243 ± 9.5 (230–256)	252 ± 17.2 (232–288)	247 ± 9.6 (231–256)	256 ± 11.4 (244–274)	251 ± 32.0 (226–287)	—	—[c]
Subadults	0	2	4	3	2	3	3	3	3	0
CL (mm)	—	196 ± 17.0 (184–208)	187 ± 16.1 (171–209)	190 ± 11.9 (180–203)	188 ± 8.5 (182–194)	194 ± 6.1 (187–199)	196 ± 6.9 (188–200)	199 ± 5.9 (192–203)	202 ± 9.5 (192–211)	—
Inconclusive	0	0	0	0	0	1	1	2	2	4

[a] Excludes females of inconclusive reproductive status.
[b] Excludes one clutch retained from the previous year, including those to which additional eggs were added (no. 1 in 2000 and 2004).
[c] Did not calculate clutch frequency due to high proportion of females of inconclusive reproductive status.
[d] Excludes one clutch laid before radiographic data were obtained.
[e] Weighted means: clutch frequency = 0.61, clutch size = 5.2 eggs, egg width = 36.1 mm.

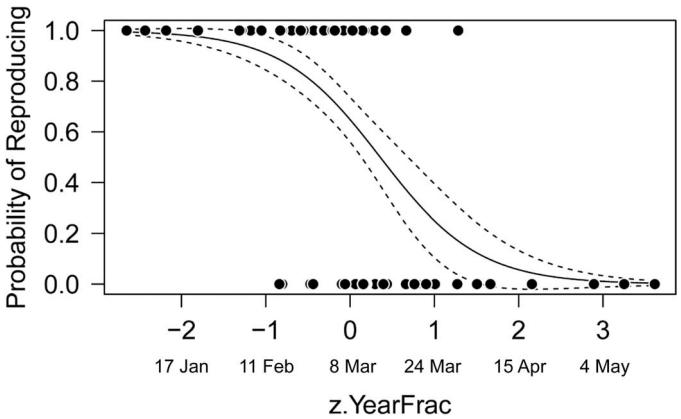

FIG. 3.—Probability of producing eggs, with 85% confidence limits, relative to timing of hibernation emergence (z.YEARFRAC) by Sonoran Desert Tortoises at Sugarloaf Mountain, Arizona. Model $R^2 = 0.28$. Unstandardized sample mean YEARFRAC = 0.18 (±0.09 SD).

about one-third as much as emergence from hibernation ($\hat{\beta}_{z.CL} = 0.52$, 85% CI = 0.08 to 1.01). Females that emerged earlier were more likely to produce eggs (Fig. 3). The probability of reproducing declined negligibly until about 11 February. However, by the mean timing of emergence in early March, the probability of producing eggs dropped to approximately 60%, and by 1 April the probability had dropped to 32% (Fig. 3). Only one tortoise that emerged later than March reproduced that season (no. 25 emerged on 17 April 1998; $n = 17$ across all years).

The prior year's reproductive status ($n = 69$) and female body condition ($n = 78$) did not predict whether a female produced eggs. The top model in each analysis included only emergence date and body size, and only more complex models included prior reproductive status and body condition.

Clutch size.—Mean clutch size varied by more than 50% among years (3.8 to 5.8 eggs; Table 3). The best climate model ($\Delta AIC_c = -3.01$) had no significant effects of rainfall and body size ($P_{rainfall} = 0.182$, $P_{z.CL} = 0.181$, $n = 74$). Clutch size also was not affected by emergence date ($P_{z.YEARFRAC} = 0.972$, $n = 60$) or previous reproductive status ($P_{c.PREREPRO} = 0.145$, $n = 47$). However, body condition had a positive effect on clutch size ($\hat{\beta}_{z.BCI} = 0.63$, 85% CI = 0.34 to 0.91, $R^2 = 0.16$, $n = 56$; Fig. 4).

Egg width.—Mean egg width varied little (≤6%) among years, ranging from 35.0 to 37.1 mm (Table 3). Model results initially indicated a positive linear effect of mean daily temperature between 10 December and 31 January ($\hat{\beta}_{temperature} = 0.29$, 85% CI = 0.13 to 0.45; $\Delta AIC_c = -3.19$), but this effect was spurious ($P_c = 0.353$, $n = 73$). Larger females produced larger eggs ($\hat{\beta}_{z.CL} = 0.86$, 85% CI = 0.55 to 1.18), but clutch size ($\hat{\beta}_{z.CSize} = 0.12$, 85% CI = –0.06 to 0.31) did not affect egg width.

We retained body size in the emergence-date analysis, and the emergence-date model differed in AIC_c by –6.37 compared to the model without ($n = 59$). Females that ended hibernation earlier produced wider eggs than did females emerging later ($\hat{\beta}_{z.YEARFRAC} = -0.38$, 85% CI = –0.56 to –0.20; $R^2_{[m]} = 0.40$, $R^2_{[c]} = 0.73$).

The prior year's reproductive status ($n = 45$) did not explain egg width; the more complex c.PREREPRO model had

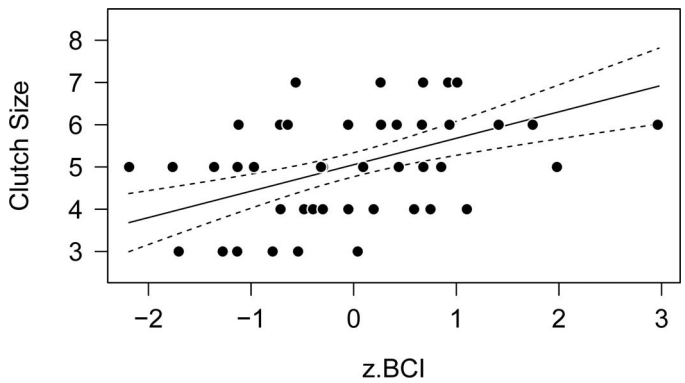

Fig. 4.—Clutch size and 85% confidence limits for Sonoran Desert Tortoises at Sugarloaf Mountain, Arizona, relative to standardized body condition index (z.BCI). Model $R^2 = 0.16$. Unstandardized sample mean BCI = 0.17 (±0.01 SD).

a larger AIC_c than the model containing only carapace length and emergence date. In the body-condition analysis, models with and without z.BCI differed in ΔAIC_c by only 2.8 (n = 46; $R^2_{[m]} = 0.59$, $R^2_{[c]} = 0.73$ for the global model that included z.BCI). Model averaging indicated that females in better condition produced larger eggs than did females in poorer condition. In this model, female size had the greatest influence on egg size (i.e., width: $\hat{\beta}_{z.CL} = 0.88$, 85% CI = 0.60 to 1.17; Fig. 5A), female body condition had less than half the effect ($\hat{\beta}_{z.BCI} = 0.38$, 85% CI = 0.04 to 0.73; Fig. 5B), and emergence date had the smallest (and inverse) effect ($\hat{\beta}_{z.YearFrac} = -0.27$, 85% CI = –0.47 to –0.06; Fig. 5C).

Discussion

We describe the most detailed study of reproduction in Sonoran Desert Tortoises. Radiographic studies of other populations in southern Arizona were all ≤2 yr (Granite Hills, Pinal County, Averill-Murray 2002a; Rincon Mountains, Pima County, Stitt 2004; Maricopa Mountains and Espanto Mountain, Maricopa County, Wirt and Holm 1997), and there have been no studies in Mexico. We also report the first examination of the female reproductive cycle in *G. morafkai*. Our results are strikingly different than those reported from studies of the closest relative of *G. morafkai*, *G. agassizii*. These differences indicate that the two species have adopted different life history strategies to persist in their different yet still harsh desert environments.

Reproductive Cycle

The common female reproductive cycle in temperate chelonians begins with vitellogenesis in late summer or fall and, after a break during hibernation, continuing until completion in spring (Kuchling 1999). However, *G. morafkai* vitellogenesis typically began in winter during our study, followed by substantial follicular growth during spring after emergence from hibernation. Maximum follicle diameter infrequently exceeded 2 cm prior to hibernation. Changes in summer follicle volume were twice as variable in those forgoing egg production than in those that had produced eggs, although there was no net summer vitellogenesis for either group. Follicles did not reach ovulatory size (ca. 2.5 cm) until spring. This contrasts with predominantly fall

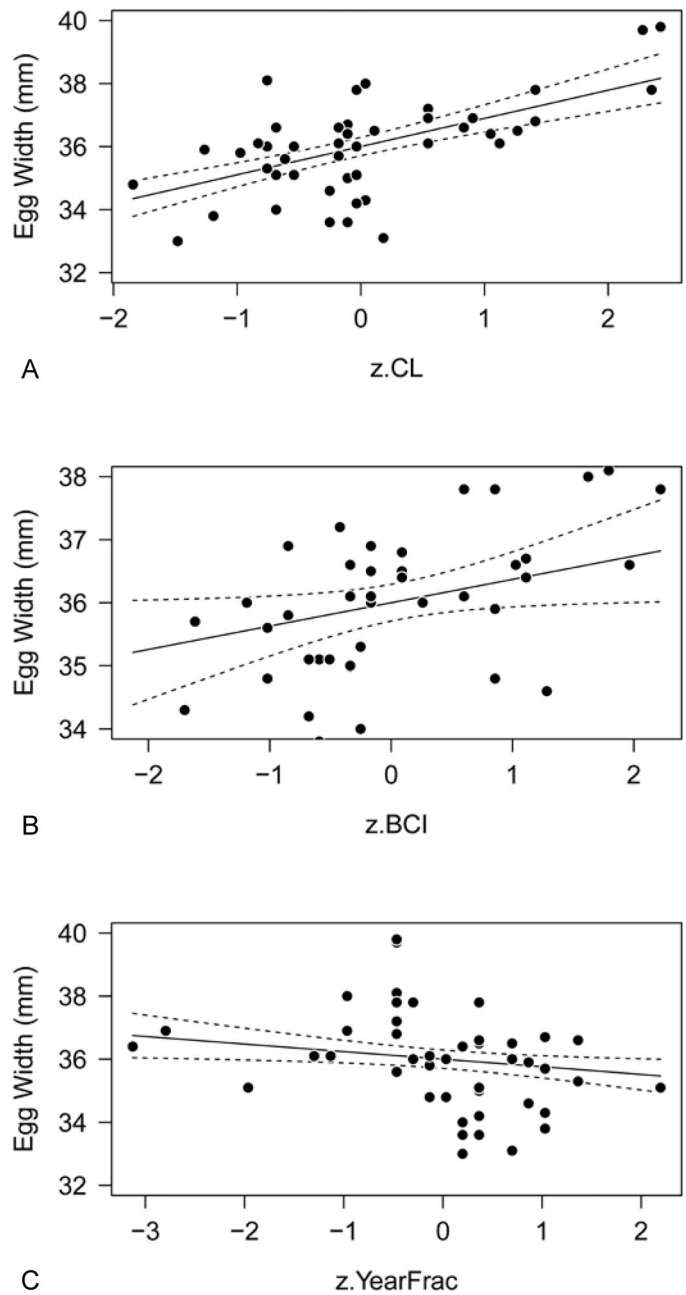

Fig. 5.—Mean egg width and 85% confidence limits for Sonoran Desert Tortoises at Sugarloaf Mountain, Arizona, relative to A, body size (z.CL); B, body condition (z.BCI); and C, emergence from hibernation (z.YearFrac). $R^2_{(m)} = 0.58$ and $R^2_{(c)} = 0.72$ for the global model, EggWidth ~ z.CL + z.YearFrac + z.BCI + (1 | Tortoise ID). Unstandardized sample means (±SD): CL = 255.5 (±13.8), BCI = 0.18 (±0.01), YearFrac = 0.16 (±0.06).

maturation previously thought to occur among species of *Gopherus*, among which winter vitellogenesis previously has not been documented (Rostal 2014). Nonetheless, roughly three-fourths of follicular growth in our *G. morafkai* occurred in the spring (36.0 cm^3 vs. 9.8 cm^3 in winter).

A similar pattern was documented in Western Swamp Turtles (*Pseudemydura umbrina*), which initiate vitellogenesis during aestivation, continuing when the females become active and start feeding (Kuchling 1999). Energy and matter allocated to *P. umbrina* follicles during dormancy presum-

ably comes entirely from stored body lipids, which is consistent with our observation of greater follicular growth during hibernation by *G. morafkai* in better condition. In contrast to *G. morafkai*, though, *P. umbrina* develops follicles more than halfway during the dormant period (Kuchling 1999).

Despite these general patterns, reproductive cycles were highly variable among females and years at Sugarloaf Mountain. For example, half of the females that developed follicles of near-ovulatory size failed to reproduce during that season. Except in 2001, when annual rainfall was above long-term averages, all ultrasonography years had below-average annual and winter rainfall (Table 1). Consequently, the low rainfall (and qualitatively, plant biomass) probably constrained females' ability to develop follicles and eggs (as for *G. agassizii*; Turner et al. 1987; Henen 1997; Lovich et al. 2015). Similarly, *P. umbrina* might resorb all ovarian follicles in years lacking sufficient food resources to ovulate (Kuchling and Bradshaw 1993). Mojave Desert Tortoises also resorb follicles (Rostal et al. 1994; B.T. Henen, personal observation), so *G. morafkai* is probably able to resorb follicles.

In contrast, almost two-thirds of egg-producing females at Sugarloaf either had no detectable follicles, or had follicles at diameters <2 cm, during the spring immediately prior to the period of ovulation. Some small follicles might have been missed in ultrasound scans, and dehydrated tortoises during the dry years of sampling might also have had less-effective ultrasound transmission (Henen and Hofmeyr 2003; B.T. Henen and M.D. Hofmeyr, personal observations), but small follicles would also require the greatest amount of vitellogenesis to become yolks. Also, these tortoises might have occupied sufficiently productive home ranges, even during dry periods, that enabled them to forage and rapidly develop follicles. Our equivocal support for this hypothesis included the tendency for females that produced eggs from small follicles to be more active in spring than females that failed to produce eggs from follicles of similar small size.

More detailed study of activity, foraging, and resource allocation to reproduction is needed to clarify factors that cause female *G. morafkai* to terminate reproductive investment already initiated and that contribute to rapid investment in the spring. Study of individual microclimate temperatures, particularly within winter hibernacula, also might help explain additional variation in follicle development. Temperature affects follicle development in a diversity of chelonians (Ganzhorn and Licht 1983; Mendonça 1987; Sarkar et al. 1996; Weber et al. 2011), but we lacked data from enough years to adequately test for effects in our population (Bailey and van de Pol 2016; van de Pol et al. 2016). Given differences in depth of hibernacula, winter activity, and spring emergence among females, we might expect a negative relationship between follicle development and winter and/or spring temperatures (cf. Rollinson et al. 2012).

We documented prematuration ovarian cycling, as seen in *P. umbrina* (Kuchling 1999), in subadult tortoises with CL as small as 186 mm. The minimum size of reproduction might be determined by a complex interaction of nutrient reserves and experience. Small or young females might require more than one year of ovarian cycling to become reproductively competent (i.e., successfully ovulate and oviposit viable eggs; Kuchling 1999; B.T. Henen, T.E. Christopher, and O.T. Oftedal, personal observations on *G. agassizii*). The only other population that has had tortoises sampled smaller than 220 mm CL was at the Granite Hills, Pinal County, Arizona, in 1997 ($n = 7$; Averill-Murray 2002a). Additional sampling is required to more precisely determine size at maturity in *G. morafkai*, which is an important measure for understanding population dynamics and generation times necessary for status assessments such as the International Union for Conservation of Nature Red List (IUCN 2000).

The smallest reproductive female *G. agassizii* had CL = 178 mm (Turner et al. 1987), indicating that *G. morafkai* might mature at larger sizes than do *G. agassizii*. The size difference between species might be related to the different amounts and predictabilities of the species' rainfall and food availability (Germano 1993; Wallis et al. 1999; Averill-Murray et al. 2014). The less predictable conditions for *G. agassizii* might prompt them to reproduce at smaller (and possibly younger) stages than do *G. morafkai*; *G. agassizii* might have higher risk of mortality and might be under selection for earlier reproduction in their life history. The more predictable resources for *G. morafkai* might enable them to grow larger before reproducing, with advantages of being more likely to reproduce, and producing wider eggs, than small females produce.

At the opposite extreme, tortoise 14 never developed follicles or eggs during 6 yr of sampling, so she might have been reproductively senescent. She had a worn carapace relative to others, consistent with old age, and she did not grow during 11 yr: 249 mm CL on 26 October 1991 to 247 mm CL on 2 August 2002. However, lacking any prior documentation of egg production, we cannot rule out other possible causes of infertility. Evidence for senescence in turtles is typically weak to nonexistent (Congdon et al. 2003; but see Warner et al. 2017), and only robust, longer-term research will determine whether this is an isolated or extreme case.

Reproductive Output

Body size and condition.—Body size is not a consistent predictor of reproductive traits among species of North American tortoises (Averill-Murray et al. 2014), and body size did not predict clutch size in Sonoran Desert Tortoises at Sugarloaf Mountain. Female size usually explains relatively little variation in the number of eggs in clutches of other North American tortoises (Landers et al. 1980; Mueller et al. 1998; Rostal and Jones 2002; Ashton et al. 2007; Rothermal and Castellón 2014). For example, in the multi-clutching *G. agassizii*, clutch size correlated weakly with female body size (Karl 1998, $R^2 \leq 0.42$; Wallis et al. 1999, $R^2 = 0.22$) or not at all (Lovich et al. 2015; Sieg et al. 2015), although the correlation was stronger in southwestern Utah (McLuckie and Fridell 2002, $R^2 = 0.57$). However, body size might determine other reproductive measures in *G. agassizii*, such as egg width and clutch volume (Wallis et al. 1999; Ennen et al. 2017), clutch frequency (Turner et al. 1986; Karl 1998; Wallis et al. 1999), clutch timing (Wallis et al. 1999), and total annual fecundity (Karl 1998; Mueller et al. 1998; Wallis et al. 1999; Lovich et al. 2015). Likewise, we found that larger females were more likely to produce eggs, and they produced larger eggs.

The body-size influences on egg size in *G. agassizii* and other chelonians indicate morphological constraints (e.g., pelvic canal or caudal gap) on egg size (Congdon and Gibbons 1987; Wallis et al. 1999; Clark et al. 2001; Hofmeyr et al. 2005; Ennen et al. 2017). However, pelvic apertures widened more steeply than did eggs, relative to female carapace length, in the Sugarloaf population of *G. morafkai* and a population of *G. agassizii*, and the largest eggs in both populations were narrower than the smallest pelvic apertures, indicating little or no pelvic constraint on egg width (Ennen et al. 2017). Nevertheless, the strong relationship between egg width and female size (CL) indicates there are other benefits of reproducing at larger sizes and highlights the evolutionary pressure for small females to begin producing eggs (Congdon and Gibbons 1987; Hofmeyr et al. 2005; Escalona et al. 2018).

The lack of a relationship between clutch size and body size in our *G. morafkai* population contrasts with allometric relationships in both egg size and clutch size in Common Map Turtles (*Graptemys geographica*), where larger females had larger egg and clutch sizes (Ryan and Lindeman 2007). *Gopherus morafkai* might be forced by the nutrient limitations imposed by the desert environment (Louw and Seely 1982; Henen 1994, 1997), especially given the short period to acquire necessary nutrients following hibernation. This short period and the paucity of rain in late spring might limit their ability to forfeit life-saving nutrients for reproduction; there seems to be a trade-off between survival and reproductive effort (Henen 1997).

Investment per offspring (e.g., egg size as a proxy) is probably not determined solely by maternal body size, but largely and directly by maternal nutritional status or condition (Henen 1997, 2002a, 2004), which is hypothesized to be correlated with body size (Rollinson and Rowe 2015). In support of this hypothesis, we found that several reproductive measures correlated to maternal body condition. Better-conditioned females experienced greater follicle growth during winter, produced more eggs per clutch, and produced wider eggs than did females in poorer condition. Similarly, gravid Speckled Padlopers (*Homopus signatus*) had higher spring body condition than did nongravid females, and better body condition might have contributed to larger egg size in dry years (Loehr et al. 2011). Due to the strong influence of hydration state and gut fill on tortoise body mass and mass-to-size condition indices (Jacobson et al. 1993; Nagy et al. 2002; Loehr et al. 2004; Hofmeyr et al. 2017), such indices are crude compared to body composition measures (Henen 1994, 1997). Consequently, we recommend future studies evaluate indices of muscle and lipid stores (e.g., USFWS 2016) or more elaborate measures of body size and condition (e.g., Loehr et al. 2004, 2010; Hofmeyr et al. 2017).

Body reserves of nonlipids (likely protein) and water were strong determinants of *G. agassizii* egg production in a drought year (Henen 1994, 1997). However, reproductive parameters in *G. agassizii* were not correlated to body condition indices during 2 yr of abundant spring forage (Wallis et al. 1999). This indicates that, in food-abundant years, nutrient intake might influence reproduction as much as or more than do nutrient reserves (Henen 2004). More detailed nutrient budgets (e.g., Henen 1994, 1997) for *G. morafkai* should clarify how their clutch size appears independent of body size, but reproductive measures certainly depend on body condition to varying degrees.

Rainfall, primary production, and diet.—Above a minimum threshold, primary production, and thus food availability for Sonoran and Mojave desert tortoises, is directly related to precipitation (Webb et al. 1978; Turner and Randall 1989; Oftedal 2002). In *G. agassizii*, the biomass of winter annuals can affect clutch frequency (Turner et al. 1986; Lovich et al. 2015) or annual egg production (Henen 1994, 1997; Wallis et al. 1999). First-clutch egg volume was greater for females at a high plant-productivity site than at a low-productivity site in the same valley and year (Sieg et al. 2015). El Niño winter rains stimulated considerable winter annual biomass and caused peak egg production for at least three *G. agassizii* populations (Turner et al. 1986; Wallis et al. 1999; Lovich et al. 2015). Similarly, most Desert Box Turtles (*Terrapene ornata luteola*) deferred reproduction in a dry spring compared to a wet spring (Nieuwolt-Dacanay 1997), and a greater proportion of *H. signatus* reproduce following wetter months (Loehr et al. 2011).

The first 4 yr of this study indicated that the rainfall-primary production relationship translated to an increased likelihood of female *G. morafkai* producing eggs following wet winters and springs (Averill-Murray 2002a). In contrast to these initial results, however, we found much less evidence of an effect of rainfall on measures of reproductive output in the 10-yr dataset. Apparently significant effects of rainfall on the probability of reproducing and on egg width were unreliable based on the large proportion of windows that were included in the 95% confidence set of tested models, spanning November through July. The predefined early spring window of 1 March through 30 April used by Averill-Murray (2002a) indicated a significant effect on the probability of reproducing at the 85% level (85% CI = 0.05 to 0.91), but confidence intervals at 90% and above overlapped zero. The large proportion of models in the confidence set might have resulted from a lack of a true climate signal, or a real climate signal that simply was too weak to emerge from a precise temporal window (van de Pol et al. 2016; Bailey and van de Pol 2016).

An asymptotic relationship between reproductive output and annual plant biomass indicates that other factors, such as body size, summer rainfall, and food consumption prior to winter dormancy, also affect reproductive output the ensuing spring (Henen 1997; Henen and Oftedal 1998; Lovich et al. 2015). Although nutritional ecology is extremely complex and understudied (e.g., Robbins 1993; Kabigumila 2001; Oftedal 2002; Henen et al. 2005), the invasion of nonnative plants, especially annual Mediterranean grasses (e.g., Brooks and Berry 2006), may reduce the availability of quality forage for desert tortoises. Invasive grasses can have less nutritional value than native forbs for juvenile *G. agassizii* (Nagy et al. 1998; Hazard et al. 2009) and if a large component of the diet, can reduce calcium assimilation, body condition, health, and survival (Hazard et al. 2010; Drake et al. 2016).

However, subadult and adult *G. agassizii* vary diet among seasons, balancing nutrient budgets on annual scales (Nagy and Medica 1986; Peterson 1996; Henen 1997), and eat soils to bolster mineral intake (Marlow and Tollestrup 1982; Esque and Peters 1994). Adult female *G. agassizii* can also store lipids, which support winter metabolism, vitellogenesis, and ensuing egg production, on summer diets composed

principally (i.e., 70% to 99%) of dry *Schismus barbatus*, an invasive, nonnative grass (Henen 1997, 2002a). In contrast, while nonnative invasives *Bromus rubens* and *S. barbatus* were common at Sugarloaf (e.g., senescent *B. rubens* was the most common annual plant sampled at a site 1.6 km from Sugarloaf in summer 1992; Murray 1993), these species comprised <3% of bites consumed by *G. morafkai* at Sugarloaf during April 2003 and September 2004 (Oftedal, undated) and were infrequently consumed in many other populations of *G. morafkai* (Van Devender et al. 2002).

Winter activity and emergence from hibernation.—Despite the lack of correlation between seasonal rainfall and reproductive output, there is considerable reproductive motive for *G. morafkai* females to emerge from hibernation early and forage. Females were more active and foraged more than males during winter at Sugarloaf and two other Sonoran Desert sites (Sullivan et al. 2014). In another population, females typically hibernated in shallower burrows than males, experienced lower winter temperatures, experienced a greater range in winter temperatures, terminated hibernation earlier and were more active in spring, and spent more time foraging in spring (Bailey et al. 1995). In contrast, there were no apparent differences in hibernation temperature (and possibly emergence) between males and females in multiple populations of *G. agassizii* (Nussear et al. 2007). Winter in the Sonoran Desert is warmer than the Mojave Desert (Turner and Brown 1982), and adult Mojave tortoises are typically inactive unless they are dehydrated and emerge to a drought-breaking rain (Berry et al. 2002; B.T. Henen, personal observation).

Female tortoises at Sugarloaf that ended hibernation later produced relatively small eggs, if any. A 2-wk delay would result in eggs about 0.2 mm smaller in diameter. Based on the average egg width (36.1 mm) and egg volume (30.8 cm^3) for this population (Averill-Murray et al. 2014), eggs laid 2 wk later would be about 1.3% smaller in volume, potentially with an associated reduction in offspring survival (see below). That some *G. morafkai* females forgo egg production by emerging later in the spring is perplexing given their ability to develop follicles quickly from winter and spring forage. Calculating energy and water budgets could clarify whether vitellogenesis is limited by maximum metabolism during this period.

Postemergence temperatures, as measured by mean degree-day accumulation, influenced clutch phenology in our *G. morafkai* population and in a *G. agassizii* population; development and laying of clutches was delayed significantly in cool years relative to warm years (Lovich et al. 2012, 2017). Appearance of eggs on radiographs occurred after ambient temperatures reached a 14-d average of 25.8°C for *G. morafkai*, and the total heat-unit accumulation was much greater than for *G. agassizii* (Lovich et al. 2017). Cooler temperatures might limit early-spring activity and, especially for *G. morafkai*, delay foraging and subsequent egg development. In contrast, other tortoises are known to be active, grow follicles, ovulate, and oviposit during winter (Hofmeyr 2004; Loehr et al. 2004; Hofmeyr et al. 2012). Longer-term investigation of follicle growth relative to temperatures, especially during or near the end of hibernation in *Gopherus* spp., might reveal influences on vitellogenesis and the preparation of eggs (cf. Sarkar et al. 1996).

Life History

In many chelonians, negative correlations between egg size and clutch size indicate an evolutionary trade-off in which females allocate nutrients to large eggs in small clutches or to small eggs in large clutches (Elgar and Heaphy 1989; Iverson et al. 1993; but see Ryan and Lindeman 2007). Some southern African testudinids carry this trade-off to an extreme, with large eggs (up to 12% of body volume) produced in single-egg clutches by females in arid habitats with unpredictable rainfall (Hofmeyr et al. 2005). Their female congeners in mesic and more predictable rainfall habitats produce more eggs (clutch size = 1 to 5) that are relatively small (only 2% to 4% of body volume) compared to the single-egg/clutch species (Hofmeyr et al. 2005). In contrast, relationships between clutch size and egg size are not consistent among North American tortoises (Averill-Murray et al. 2014) or Desert Box Turtles (Nieuwolt-Dacanay 1997), although clutch size was negatively correlated to egg width in *G. polyphemus* (Averill-Murray et al. 2014; but see Rothermal and Castellon 2014). Also, egg length and volume were negatively correlated with the size of first clutches, and egg width decreased in successive intraseason clutches, in *G. agassizii* (Wallis et al. 1999; Ennen et al. 2017).

An inverse relationship between body-size–adjusted clutch frequency and clutch mass (or clutch volume) indicates a trade-off between producing many small clutches or few large clutches (Iverson 1992). This trade-off manifests with chelonians in more predictable environments reproducing less often than those in less predictable environments and occurs in North American tortoises (Iverson 1992; Hofmeyr et al. 2005; Averill-Murray et al. 2014). *Gopherus agassizii* experiences the lowest amount, greatest seasonality, and the greatest annual variation of annual precipitation among North American tortoises (Germano 1993), yet has the greatest average clutch frequency and annual fecundity among *Gopherus* spp. (Averill-Murray et al. 2014). For example, *G. agassizii* females produce more and larger eggs per year than do *G. morafkai* females (Averill-Murray et al. 2014; Ennen et al. 2017). Precipitation within the range of *G. morafkai*, which lays a maximum of one clutch per year, is about 80% greater and more predictable than within the range of *G. agassizii* (Germano 1993). Thus, the reproductive differences between *G. morafkai* and *G. agassizii* are consistent with the predictability of rainfall they experience.

Food availability and reliability have been invoked to explain the adaptive basis of capital- and income-breeding strategies, which represent two ends of a spectrum (Drent and Daan 1980; Stephens et al. 2009). Capital breeders store nutrients for later reproduction, and income breeders use nutrients acquired during the reproductive period (Drent and Daan 1980; Stearns 1992). Capital breeding might be the predominant strategy in ectotherms, especially chelonians, because vitellogenic periods are so lengthy (Kuchling 1999; Henen 2004) and the total volume of reproductive output is constrained by the maternal body volume. Also, because most of the nutrient and energy investment is contained in the clutch at oviposition or hatching (Henen 1997), increased allocation of nutrients after the initial allocation at ovulation might be impossible even if extra resources are available (Bonnet et al. 1998). The cost of

reproduction should be evaluated over the time period over which energy is expended with respect to a single reproductive event (Congdon et al. 1982; Henen 1997; Stephens et al. 2009). For the following discussion, this occurs over an annual period, from the end of one nesting season to the beginning of the next.

The reproductive strategy of *G. agassizii* is intermediate to the capital and income strategies (Henen 2002a,b; 2004). *Gopherus agassizii* females increase their body energy content before winter and use reserves the following spring to produce eggs (Henen 1997), and annual egg production is correlated with the previous year's nitrogen intake (Henen and Oftedal 1998; Henen 2002b). This timing also is reflected in vitellogenesis occurring mostly before hibernation (Rostal et al. 1994; Henen and Oftedal 1998). However, *G. agassizii* females also acquire energy by foraging during spring when resources are available, which can contribute to production of additional clutches during the reproductive season (Henen 1997; Henen and Oftedal 1998; Lovich et al. 1999). Only in unusual cases do *G. agassizii* forgo egg production due to poor body condition (protein and water reserves) or poor conditions of spring forage (Henen 1997; Lovich et al. 1999). Western Swamp Turtles allocate most nutrients to follicles when females are dormant (capital strategy), but require immediate harvest of large amounts of resources to ovulate and produce eggs (income strategy; Kuchling 1999). Wallis et al. (1999) also found that small *G. agassizii* lay eggs later in the spring and produce fewer clutches than do large tortoises, presumably because smaller tortoises have fewer body reserves and rely upon spring forage for reproduction. Consequently, the capital–income strategy can vary even within a population.

Sonoran Desert Tortoises fall closer to the income-breeding end of the spectrum than do Mojave Desert Tortoises. Compared to female *G. agassizii*, female *G. morafkai* invested less in vitellogenesis before winter, with most occurring after emergence from hibernation. Fall follicles in *G. morafkai* (ca. 1 to 1.5 cm diameter) represent only 25% to 50% of the volume of *G. agassizii* prewinter follicles, which have diameters of 2 cm (Rostal et al. 1994; Henen and Oftedal 1998). A large proportion of *G. morafkai* females in this study produced eggs after showing small or no ovarian follicles in early spring, so they must be allocating resources faster toward immediate reproduction than do *G. agassizii* females in spring (Henen and Oftedal 1998).

Emerging early from hibernation increased the likelihood of producing eggs and resulted in production of larger eggs than females that emerged later, probably via a longer prereproductive foraging window. The Arizona Upland Subdivision of the Sonoran Desert contains greater plant diversity, cover, and primary production than the Mojave Desert, with plant cover reaching 60% to 80% in some areas and with spring annuals more numerous than summer annuals (Hadley and Szarek 1981; Crosswhite and Crosswhite 1982). Only in the driest years might it be worthwhile for many *G. morakfai* females to extend hibernation. For example, the latest mean date of emergence among adult females was for non–egg layers in 2000, which followed a very dry winter (Tables 1, 2). We also note that the body-size influences on whether a female reproduced, and of body condition on follicle growth over winter, indicate that some energy reserves contributed to reproduction.

Capital breeding is advantageous in environments with unpredictable food availability, such as that occupied by *G. agassizii*, whereas income breeding is favored in more predictable and productive environments such as the Arizona Upland Subdivision of the Sonoran Desert (Jönsson 1997). A main benefit of capital breeding is that nutrients can be acquired when available and it is most efficient (e.g., as unpredictable resources become available), but income breeders might expend more energy in short periods (e.g., high field metabolic rates; Bonnet et al. 1998) to obtain the necessary energy for reproduction. The critical measures to quantify the degree of capital or income breeding are the total reproductive expenditure and metabolizable intake of nutrients, relative to changes in stored reserves, over the relevant periods of the reproductive cycle (Congdon et al. 1982; Henen 1997; Stephens et al. 2009). Extending the current study to field measurement of energy expenditure and intake with nondestructive methods, including gas dilution, doubly labeled water, ultrasonography, and X-radiography, would determine whether seasonal and annual metabolic rates and energy allocation differ between these two species of desert tortoises (cf. Henen 2002b).

Finally, strong selection pressure in chelonians for large eggs has been posited to confer survivorship advantages to the eggs and hatchlings (see Janzen et al. 2000; Nafus et al. 2015). Optimal egg size theory states that females should make the largest eggs that maximize offspring fitness, while varying the number of eggs in a reproductive bout (Smith and Fretwell 1974). However, observed patterns in both *G. morafkai* and *G. agassizii* differed from predictions of this theory (Wallis et al. 1999; Ennen et al. 2017). One explanation for apparently suboptimal allocation of resources to reproduction relates to the environment each species inhabits.

The relatively predictable summer precipitation in the Sonoran Desert's Arizona Upland allows *G. morafkai* hatchlings to emerge in late summer to a productive environment in which they can reliably obtain forage, thereby allowing females to produce smaller eggs than otherwise possible. Similarly, females in an eastern Mojave population of *G. agassizii* produced smaller eggs in larger second clutches (with higher annual egg production) than the larger eggs and smaller second clutches (and lower annual egg production) of females in a western Mojave population that had less predictable summer precipitation and forage; the total egg volume was similar between populations (Wallis et al. 1999). There might be diminishing returns in producing larger eggs (i.e., not proportionate increases in offspring fitness) in more predictable or productive environments, so it might be prudent to conserve some of those resources for subsequent maternal survival and possibly reproduction.

Also, *G. morafkai* produces eggs of relatively uniform width within females (4% coefficient of variation [CV]) and among years (3% CV), which is consistent with a conservative bet-hedging strategy that ensures offspring are well provisioned in most environmental conditions, including infrequent poor years (Philippi and Seger 1989; Einum and Fleming 2004; Ennen et al. 2017). Under less-predictable conditions, *G. agassizii* might combine within-generation bet hedging (spreading clutches spatially and temporally within a season) with a strategy that differentially allocates resources

among clutches (Ennen et al. 2017). Third-clutch eggs in *G. agassizii* were similar in size to *G. morafkai* eggs, indicating similar provisioning for *G. agassizii* eggs for hatchlings emerging during a time of more predictable forage later in the year; resources too depleted to produce larger third-clutch eggs; or differential provisioning of eggs based on sex-specific differences in hatchling fitness resulting from seasonal differences in temperature-dependent sex determination (Ennen et al. 2017). More study is required to discern fitness differences between clutches.

Management Implications

Capital- and income-breeding strategies represent different linkages between organisms and their environment (Drent and Daan 1980; Stephens et al. 2009). The reliance on stored reserves by capital breeders is likely to result in greater lags in associations with environmental factors than in species that finance reproduction using currently available resources (income). Understanding relationships between productivity and environmental factors is important in managing responses of populations to environmental change. For example, a capital breeder's strategy to store energy for reproduction might facilitate its ability to cope with an increasingly unpredictable environment, whereas an income breeder accustomed to reliable forage fares badly in unpredictable environments. A large change in resource phenology might also have a greater impact on income breeders than on capital breeders if the resources necessary for reproduction are no longer available during the narrow periods income breeders need them (Stephens et al. 2009).

The different positions along the capital:income breeding spectrum occupied by *G. agassizii* and *G. morafkai* indicate different implications for these species in the face of climate change. The southwestern United States is expected to undergo severe aridification in the 21st century (Seager et al. 2007; Ault et al. 2014; Cook et al. 2015), and from our capital vs. income predictions about forage availability and use, we might expect *G. agassizii* to fare better than *G. morafkai* due to the former already possessing traits that have enabled it to endure a less predictable and less productive climate (Turner and Brown 1982; MacMahon 1990; see exaptation and adaptation below). However, niche models indicate that *G. agassizii* might experience 55% to 88% reduction in its habitat near the interface of the Sonoran and Mojave deserts in southern California (Barrows 2011; Barrows et al. 2016). Simultaneously, the range of *G. morafkai* in Arizona is predicted to change little by 2099 (van Riper et al. 2014). These predictions are based on projected mean temperatures, which correlate negatively with precipitation (Barrows et al. 2016). It is unclear how either species might respond to potential changes in phenology of preferred forage plants or to changes in physiological triggers for spring emergence or reproductive cycles (Lovich et al. 2012, 2017).

The allometric egg size–body size relationship of *G. morafkai* indicates that females might have the capacity to increase provisions to their offspring, perhaps at a cost of reduced clutch size or clutch frequency (i.e., fewer gravid females per year); this change might help females counter aridification-based decreases in forage availability. *Homopus signatus* females are already extreme in producing just one large egg per clutch in their harsh, unpredictable, and arid environment, and they might be vulnerable to aridification that is predicted to exacerbate their climate (Hofmeyr et al. 2005; Loehr et al. 2010). Such a response in *G. morafkai* would be more direct than adopting the multi-clutch strategy of *G. agassizii*, especially under a relatively rapid rate of climate change. A final alternative of producing more eggs of the same size is even less likely to maintain parental fitness with same-sized hatchlings subjected to an increasingly harsh environment.

Other factors besides reproductive strategies, such as dehydration or starvation, might determine the fate of desert tortoises. For example, survival of *G. agassizii* is partially contingent upon a combination of exaptations that evolved long before its desert habitat (Bradshaw 1997; Morafka and Berry 2002), such as large, semipermeable bladders (Dantzler and Schmidt-Nielsen 1966); low and highly accommodating metabolic rates and water flux rates (Nagy and Medica 1986; Henen et al. 1998); a strong tolerance for desiccation and high plasma osmolalities (Nagy and Medica 1986; Peterson 1996); and a reproductive effort that accommodates extreme variation in nutrient reserves and availability (Henen 1997). Large mortality events associated with drought have been described for several populations of both species (Turner et al. 1984; Peterson 1994; Longshore et al. 2003; Esque et al. 2010; Zylstra et al. 2013; Lovich et al. 2014). Average survival of adult *G. morafkai* under projected climate-change scenarios is expected to decrease 3% in most populations during 2035 to 2060 relative to survival during 1987 to 2008 (Zylstra et al. 2013).

Episodic, drought-related periods of high mortality have probably occurred repeatedly in the evolutionary history of desert tortoises, but anthropogenic threats might exacerbate natural stresses, and recovery of populations is likely to be slow (Peterson 1994; cf. Reed et al. 2009). In fact, nutrition and survival of desert tortoises are compromised by seemingly intractable suites of anthropogenic threats, regardless of climate change (Howland and Rorabaugh 2002; Darst et al. 2013; Berry and Aresco 2014). Despite the evolution of different life history strategies in response to desert ecosystems of variable productivity and predictability, both desert tortoise species might be living so close to the edge of their physiological tolerances that they might not survive climate change without improved conservation efforts to mitigate human-caused impacts (Peterson 1994; Averill-Murray et al. 2012).

Acknowledgments.—This project was funded by a challenge cost-share agreement between the U.S. Forest Service and the University of Arizona, the Arizona Game and Fish Department Heritage Fund, and grants from the U.S. Fish and Wildlife Service and National Fish and Wildlife Foundation's Partnerships for Wildlife program. Animals were handled under the authority and protocols of the Arizona Game and Fish Department and were consistent with Beaupre (2004). This project would not have been possible without the guidance of C. Schwalbe during 1991 to 1993 and the tremendous assistance of C. Klug and J.D. Riedle. We also thank over 130 volunteers who helped transport tortoises for radiography. J. Shurtliff , D. Brondt, G. Jontz, M. Madden, R. Montano, T. Poole, and L. Smith made particularly valuable contributions to the field efforts. Union Hills Animal Clinic and Bell West Animal Hospital allowed the use of their automatic developers to develop radiographs. We thank B. Hardenbrook and the Nevada Department of Wildlife for the use of their ultrasound machine. E. Stitt allowed us to sample tortoises under his study at Saguaro National Park. L. Allison, R.J. Steidl, and E. Zylstra provided statistical advice, and L. Bailey provided advice and assistance with the climwin analyses. The manuscript was improved by the comments of three anonymous reviewers. The findings and conclusions provided in this article

are those of the authors and do not necessarily represent the views of their affiliated organizations.

Literature Cited

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 76:1175–1178.

Ashton, K.G., R.L. Burke, and J.N. Layne. 2007. Geographic variation in body and clutch size of Gopher Tortoises. Copeia 2007:355–363.

Ault, T.R., J.E. Cole, J.T. Overpeck, G.T. Pederson, and D.M. Meko. 2014. Assessing the risk of persistent drought using climate model simulations and paleoclimate data. Journal of Climate 27:7529–7549.

Averill-Murray, R.C. 2002a. Reproduction of *Gopherus agassizii* in the Sonoran Desert, Arizona. Chelonian Conservation and Biology 4:295–301.

Averill-Murray, R.C. 2002b. Effects on survival of Desert Tortoises (*Gopherus agassizii*) urinating during handling. Chelonian Conservation and Biology 4:430–435.

Averill-Murray, R.C., B.E. Martin, S.J. Bailey, and E.B. Wirt. 2002. Activity and behavior of the Sonoran Desert Tortoise in Arizona. Pp. 135–158 in The Sonoran Desert Tortoise: Natural History, Biology, and Conservation (T.R. Van Devender, ed.). University of Arizona Press and Arizona-Sonora Desert Museum, USA.

Averill-Murray, R.C., C.R. Darst, K.J. Field, and L.J. Allison. 2012. A new approach to conservation of the Mojave Desert Tortoise. BioScience 62:893–899.

Averill-Murray, R.C., L.J. Allison, and L.L. Smith. 2014. Nesting and reproductive output among North American tortoises. Pp. 110–117 in Biology and Conservation of North American Tortoises (D. Rostal, E.D. McCoy and H.R. Mushinsky, eds.). Johns Hopkins University Press, USA.

Bailey, L.D., and M. van de Pol. 2016. Climwin: An R toolbox for climate window analysis. PLOS One 11:e0167980. https://doi.org/10.1371/journal.pone.0167980.

Bailey, S.J., C.R. Schwalbe, and C.H. Lowe. 1995. Hibernaculum use by a population of Desert Tortoises (*Gopherus agassizii*) in the Sonoran Desert. Journal of Herpetology 29:361–369.

Barrows, C.W. 2011. Sensitivity to climate change for two reptiles at the Mojave–Sonoran Desert interface. Journal of Arid Environments 75:629–635.

Barrows, C.W., B.T. Henen, and A.E. Karl. 2016. Identifying climate refugia: A framework to inform conservation strategies for Agassiz's Desert Tortoise in a warmer future. Chelonian Conservation and Biology 15:2–11.

Barton, K. 2014. MuMIn: Multi-model Inference. R Package, Version 1.10.5. Available at http://CRAN.R-project.org/package=MuMIn. R Foundation for Statistical Computing, Austria.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beaupre, S.J. (ed.). 2004. Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research, 2nd edition. American Society of Ichthyologists and Herpetologists, USA.

Berry, K.H., and M.J. Aresco. 2014. Threats and conservation needs for North American tortoises. Pp. 149–158 in Biology and Conservation of North American Tortoises (D. Rostal, E.D. McCoy, and H.R. Mushinsky, eds.). Johns Hopkins University Press, USA.

Berry, K.H., E.K. Spangenberg, B.L. Homer, and E.R. Jacobson. 2002. Deaths of Desert Tortoises following periods of drought and research manipulation. Chelonian Conservation and Biology 4:436–448.

Bonnet, X., D. Bradshaw, and R. Shine. 1998. Capital versus income breeding: An ectothermic perspective. Oikos 83:333–342.

Bradshaw, S.D. 1997. Homeostasis in Desert Reptiles: Adaptations of Desert Organisms. Springer-Verlag, USA.

Brooks, M.L., and K.H. Berry. 2006. Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA. Journal of Arid Environments 67:100–124.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edition. Springer-Verlag, USA.

Cade, B.S. 2015. Model averaging and muddled multimodel inferences. Ecology 96:2370–2382.

Clark, P.J., M.A. Ewert, and C.E. Nelson. 2001. Physical apertures as constraints on egg size and shape in the Common Musk Turtle, *Sternotherus odoratus*. Functional Ecology 15:70–77.

Congdon, J.D., and J.W. Gibbons. 1987. Morphological constraint on egg size: A challenge to optimal egg size theory? Proceedings of the National Academy of Sciences USA 84:4145–4147.

Congdon, J.D., and J.W. Gibbons. 1990. The evolution of turtle life histories. Pages 45–54 in Life History and Ecology of the Slider Turtle (J.W. Gibbons, ed.). Smithsonian Institution Press, USA.

Congdon, J.D., A.E. Dunham, and D.W. Tinkle. 1982. Energy budgets and life histories of reptiles. Pages 233–271 in Biology of the Reptilia, vol. 13, Physiology D (C. Gans and F.H. Pough, eds.). Academic Press, USA.

Congdon, J.D., R.D. Nagle, O.M. Kinney, R.C. van Loben Sels, T. Quinter, and D.W. Tinkle. 2003. Testing hypotheses of aging in long-lived Painted Turtles (*Chrysemys picta*). Experimental Gerontology 38:765–772.

Cook, B.I., T.R. Ault, and J.E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1:e1400082. https://doi.org/10.1126/sciadv.1400082.

Crosswhite, F.S., and C.D. Crosswhite. 1982. The Sonoran Desert. Pages 163–319 in Reference Handbook on the Deserts of North America (G.L. Bender, ed.). Greenwood Press, USA.

Dantzler, W.H., and B. Schmidt-Nielsen 1966. Excretion in fresh-water turtle (*Pseudemys scripta*) and desert tortoise (*Gopherus agassizii*). American Journal of Physiology 2110:198–210.

Darst, C.R., P.J. Murphy, N.W. Strout, S.P. Campbell, K.J. Field, L.J. Allison, and R.C. Averill-Murray. 2013. A strategy for prioritizing threats and recovery actions for at-risk species. Environmental Management 51:786–800.

Drake, K.K., L. Bowen, K.E. Nussear, T.C. Esque, A.J. Berger, N.A. Custer, S.C. Waters, J.D. Johnson, A.K. Miles, and R.C. Lewison. 2016. Native impacts of invasive plants on conservation of sensitive desert wildlife. Ecosphere 7(10):e01531. https://doi.org/10.1002/ecs2.1531.

Drent, R.H., and S. Daan. 1980. The prudent parent: Energetic adjustments in avian breeding. Ardea 68:225–252.

Einum, S., and I.A. Fleming. 2004. Environmental unpredictability and offspring size: Conservative versus diversified bet-hedging. Evolutionary Ecology Research 6:443–455.

Elgar, M.A., and L.J. Heaphy. 1989. Covariation between clutch size, egg weight and egg shape: Comparative evidence for chelonians. Journal of Zoology, London 219:137–152.

Ennen, J.R., J.E. Lovich, R.C. Averill-Murray, C.B. Yackulic, M. Agha, C. Loughran, L. Tennant, and B. Sinervo. 2017. The evolution of different maternal investment strategies in two closely related desert vertebrates. Ecology and Evolution 7:3177–3189.

Escalona, T., D.C. Adams, and N. Valenzuela. 2018. A lengthy solution to the optimal propagule size problem in the large-bodied South American freshwater turtle, *Podocnemis unifilis*. Evolutionary Ecology 32:29–41.

Esque, T.C., and E.L. Peters. 1994. Ingestion of bones, stones, and soil by desert tortoises. Fish and Wildlife Research 13:73–84.

Esque, T.C., K.E. Nussear, K.K. Drake, . . . J.S. Heaton. 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endangered Species Research 12:167–177.

Ganzhorn, D., and P. Licht. 1983. Regulation of seasonal gonadal cycles by temperature in the Painted Turtle, *Chrysemys picta*. Copeia 1983:347–358.

Germano, D.J. 1993. Shell morphology of North American tortoises. American Midland Naturalist 129:319–335.

Gibbons, J.W., and J.L. Greene. 1979. X-ray photography: A technique to determine reproductive patterns of freshwater turtles. Herpetologica 35:86–89.

Graham, T.E., and P.J. Petokas. 1989. Correcting for magnification when taking measurements directly from radiographs. Herpetological Review 20:46–47.

Hadley, N.F., and S.R. Szarek. 1981. Productivity of desert ecosystems. BioScience 31:747–753.

Hazard, L.C., D.R. Shemanski, and K.A. Nagy. 2009. Nutritional quality of natural foods of juvenile Desert Tortoises (*Gopherus agassizii*): Energy, nitrogen, and fiber digestibility. Journal of Herpetology 43:38–48.

Hazard, L.C., D.R. Shemanski, and K.A. Nagy. 2010. Nutritional quality of natural foods of juvenile and adult Desert Tortoises (*Gopherus agassizii*): Calcium, phosphorus, and magnesium digestibility. Journal of Herpetology 44:135–147.

Henen, B.T. 1994. Seasonal and Annual Energy and Water Budgets of Female Desert Tortoises (*Xerobates agassizii*) at Goffs, California. Ph.D. dissertation, University of California Los Angeles, USA.

Henen, B.T. 1997. Seasonal and annual energy budgets of female Desert Tortoises (*Gopherus agassizii*). Ecology 78:283–296.

Henen, B.T. 2002a. Energy and water balance, diet, and reproduction of

female Desert Tortoises (*Gopherus agassizii*). Chelonian Conservation and Biology 4:319–329.

Henen, B.T. 2002b. Reproductive effort and reproductive nutrition of female Desert Tortoises: Essential field methods. Integrative and Comparative Biology 42:43–50.

Henen, B.T. 2004. Capital and income breeding in two species of desert tortoise. Transactions of the Royal Society of South Africa 59:65–71.

Henen, B.T., and M.D. Hofmeyr. 2003. Viewing chelonian reproductive ecology through acoustic windows: Cranial and inguinal perspectives. Journal of Experimental Zoology 297A:88–104.

Henen, B.T., and O.T. Oftedal. 1998. The importance of dietary nitrogen to the reproductive output of female Desert Tortoises (*Gopherus agassizii*). Proceedings of the Comparative Nutrition Society 1998:83–88.

Henen, B.T., C.C. Peterson, I.R. Wallis, K.H. Berry, and K.A. Nagy. 1998. Desert Tortoise field metabolic rates and water fluxes track local and global climatic conditions. Oecologia 117:365–373.

Henen, B.T., M.D. Hofmeyr, R.A. Balsamo, and F.M. Weitz. 2005. Lessons from the food choices of the endangered Geometric Tortoise *Psammobates geometricus*. South African Journal of Science 101:435–438.

Hinton, T.G., P. Fledderman, J. Lovich, J. 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.

Hofmeyr, M.D. 2004. Egg production in *Chersina angulata*: An unusual pattern in a Mediterranean climate. Journal of Herpetology 38:172–179.

Hofmeyr, M.D., B.T. Henen, and V.J.T. Loehr. 2005. Overcoming environmental and morphological constraints: Egg size and pelvic kinesis in the smallest tortoise, *Homopus signatus*. Canadian Journal of Zoology 83:1343–1352.

Hofmeyr, M.D., U.P. van Bloemestein, B.T. Henen, and C. Weatherby 2012. Sexual and environmental variation in the space requirements of the Critically Endangered geometric tortoise, *Psammobates geometricus*. Amphibia-Reptilia 33:185–197.

Hofmeyr, M.D., B.T. Henen, and S. Walton. 2017. Season, sex and age variation in the haematology and body condition of geometric tortoises *Psammobates geometricus*. African Zoology 52:21–30.

Howland, J.M., and J.C. Rorabaugh. 2002. Activity and behavior of the Sonoran Desert Tortoise in Arizona. Pp. 334–354 in The Sonoran Desert Tortoise: Natural History, Biology, and Conservation (T.R. Van Devender, ed.). University of Arizona Press and Arizona-Sonora Desert Museum, USA.

[IUCN] International Union for the Conservation of Nature. 2000. IUCN Red List Categories and Criteria, Version 3.1, 2nd edition. IUCN Species Survival Commission, IUCN Council, Switzerland.

Iverson, J.B. 1992. Correlates of reproductive output in turtles (Order Testudines). Herpetological Monographs 6:25–42.

Iverson, J.B., C.P. Balgooyen, K.K. Byrd, and K.K. Lyddan. 1993. Latitudinal variation in egg and clutch size in turtles. Canadian Journal of Zoology 71:2448–2461.

Jackson, D.C. 2011. Life in a Shell: A Physiologist's View of a Turtle. Harvard University Press, USA.

Jacobson, E.R., M. Weinstein, K. Berry, B. Hardenbrook, C. Tomlinson, and D. Freitas. 1993. Problems with using weight versus carapace length relationships to assess tortoise health. The Veterinary Record 132:222–223.

Janzen, F.J., J.K. Tucker, and G.L. Paukstis. 2000. Experimental analysis of an early life-history stage selection on size of hatchling turtles. Ecology 81:2290–2304.

Jönsson, K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66.

Kabigumila, J. 2001. Sighting frequency and food habits of the Leopard Tortoise, *Geochelone pardalis*, in northern Tanzania. African Journal of Ecology 39:276–285.

Karl, A.E. 1998. Reproductive Strategies, Growth Patterns, and Survivorship of a Long-Lived Herbivore Inhabiting a Temporally Variable Environment. Ph.D. dissertation, University of California Davis, USA.

Kuchling, G. 1998. How to minimize risk and optimize information gain in assessing reproductive condition and fecundity of live female chelonians. Chelonian Conservation and Biology 3:118–123.

Kuchling, G. 1999. The Reproductive Biology of the Chelonia. Springer-Verlag, Germany.

Kuchling, G., and S.D. Bradshaw. 1993. Ovarian cycle and egg production in the Western Swamp Tortoise *Pseudemydura umbrina* (Testudines: Chelidae) in the wild and in captivity. Journal of Zoology 229:405–419.

Landers, J.L., J.A. Garner, and W.A. McRae. 1980. Reproduction of Gopher Tortoises (*Gopherus polyphemus*) in southwestern Georgia. Herpetologica 36:353–361.

Lefcheck, J.S. 2015. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution. 7:573–579.

Leuteritz, T.E.J., and M.D. Hofmeyr. 2007. The extended reproductive season of Tent Tortoises (*Psammobates tentorius tentorius*): A response to an arid and unpredictable environment. Journal of Arid Environments 68:546–563.

Loehr, V.J.T., B.T. Henen, and M.D. Hofmeyr. 2004. Reproduction of the smallest tortoise, the Namaqualand speckled padloper, *Homopus signatus signatus*. Herpetologica 60:444–454.

Loehr, V.J.T., B.T. Henen, and M.D. Hofmeyr. 2010. Small and sensitive to drought: Consequences of aridification to the conservation of *Homopus signatus signatus*. African Journal of Herpetology 58:116–125.

Loehr, V.J.T., B.T. Henen, and M.D. Hofmeyr. 2011. Reproductive responses to rainfall in the Namaqualand Speckled Tortoise. Copeia 2011:278–284.

Longshore, K.M., J.R. Jaeger, and J.M. Sappington. 2003. Desert Tortoise (*Gopherus agassizii*) survival at two eastern Mojave Desert sites: Death by short-term drought? Journal of Herpetology 37:169–177.

Louw, G.N., and M.K. Seely 1982. Ecology of Desert Organisms. Longman Group Limited, USA.

Lovich, J., P. Medica, H. Avery, K. Meyer, G. Bowser, and A. Brown. 1999. Studies of reproductive output of the Desert Tortoise at Joshua Tree National Park, the Mojave National Preserve, and comparative sites. Park Science 19:22–24.

Lovich, J., M. Agha, M. Meulblok, K. Meyer, J. Ennen, C. Loughran, S. Madrak, and C. Bjurlin. 2012. Climatic variation affects clutch phenology in Agassiz's Desert Tortoise *Gopherus agassizii*. Endangered Species Research 19:63–74.

Lovich, J.E., C.B. Yackulic, J. Freilich, M. Agha, M. Austin, K.P. Meyer, T.R. Arundel, J. Hansen, M.S. Vamstad, and S.A. Root. 2014. Climatic variation and tortoise survival: Has a desert species met its match? Biological Conservation 169:214–224.

Lovich, J.E., J.R. Ennen, C.B. Yackulic, K. Meyer-Wilkins, M. Agha, C. Loughran, C. Bjurlin, M. Austin, and S. Madrak. 2015. Not putting all their eggs in one basket: Bet-hedging despite extraordinary annual reproductive output of desert tortoises. Biological Journal of the Linnean Society 115:399–410.

Lovich, J.E., R.C. Averill-Murray, M. Agha, J.R. Ennen, and M. Austin. 2017. Variation in annual clutch phenology of desert tortoises (*Gopherus morafkai*) in the Sonoran Desert of Arizona. Herpetologica 73:313–322.

MacMahon, J.A. 1990. Deserts. Alfred A. Knopf, USA.

Marlow, R.W., and K. Tollestrup. 1982. Mining and exploitation of natural mineral deposits by the Desert Tortoise, *Gopherus agassizii*. Animal Behaviour 30:475–478.

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 4:288–294.

Mendonça, M.T. 1987. Photothermal effects on the ovarian cycle of the Musk Turtle, *Sternotherus odoratus*. Herpetologica 43:82–90.

Morafka, D.J., and K.H. Berry. 2002. Is *Gopherus agassizii* a desert-adapted tortoise, or an exaptive opportunist? Implications for tortoise conservation. Chelonian Conservation and Biology 4:263–287.

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.

Murray, R.C. 1993. Mark–recapture Methods for Monitoring Sonoran Populations of the Desert Tortoise (*Gopherus agassizii*). M.S. thesis, University of Arizona, USA.

Nafus, M.G., B.D. Todd, K.A. Buhlmann, and T.D. Tuberville. 2015. Consequences of maternal effects on offspring size, growth and survival in the desert tortoise. Journal of Zoology 297:108–114.

Nagy, K.A., and P.A. Medica. 1986. Physiological ecology of Desert Tortoises in southern Nevada. Herpetologica 42:73–92.

Nagy, K.A., B.T. Henen, and D.B. Vyas. 1998. Nutritional quality of native and introduced food plants of wild Desert Tortoises. Journal of Herpetology 32:260–267.

Nagy, K.A., B.T. Henen, D.B. Vyas, and I.R. Wallis. 2002. A condition index for the Desert Tortoise (*Gopherus agassizii*). Chelonian Conservation and Biology 42:425–429.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Nieuwolt-Dacanay, P.M. 1997. Reproduction in the Western Box Turtle, *Terrapene ornata luteola*. Copeia 1997:819–826.

Nussear, K.E., T.C. Esque, D.F. Haines, and C.R. Tracy. 2007. Desert Tortoise hibernation: Temperatures, timing, and environment. Copeia 2007:378–386.

Oftedal, O.T. undated. Nutritional Ecology of the Sonoran Desert Tortoise. Heritage Grant I04004. Arizona Game and Fish Department, USA.

Oftedal, O.T. 2002. Nutritional ecology of the Desert Tortoise in the Mohave and Sonoran deserts. Pp. 194–241 in The Sonoran Desert Tortoise: Natural History, Biology, and Conservation (T.R. Van Devender, ed.). University of Arizona Press and Arizona-Sonora Desert Museum, USA.

Peterson, C.C. 1994. Different rates and causes of high mortality in two populations of the threatened Desert Tortoise, *Gopherus agassizii*. Biological Conservation 70:101–108.

Peterson, C.C. 1996. Anhomeostasis: Seasonal water and solute relations in two populations of the Desert Tortoise (*Gopherus agassizii*) during chronic drought. Physiological Zoology 69:1324–1358.

Philippi, T., and J. Seger. 1989. Hedging one's evolutionary bets, revisited. Trends in Ecology and Evolution 4:41–44.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2016. nlme: Linear and Nonlinear Mixed Effects Models. R Package, Version 3.1-128. R Foundation for Statistical Computing, Austria. Available at http://CRAN.R-project.org/package=nlme.

R Core Team. 2016. R: A Language and Environment for Statistical Computing, Version 3.3.2. Available at http://www.R-project.org. R Foundation for Statistical Computing, Austria.

Reed, J.M., N. Fefferman, and R.C. Averill-Murray. 2009. Vital rate sensitivity analysis as a tool for assessing management actions for the Desert Tortoise. Biological Conservation 142:2710–2717.

Richards, S.A., M.J. Whittingham, and P.A. Stephens. 2011. Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. Behavioral Ecological and Sociobiology 65:77–89.

Robbins, C.T. 1993. Wildlife Feeding and Nutrition. Academic Press, USA.

Rollinson, N., and L. Rowe. 2015. The positive correlation between maternal size and offspring size: Fitting pieces of a life-history puzzle. Biological Reviews 91:1134–1148.

Rollinson, N., R.G. Farmer, and R.J. Brooks. 2012. Widespread reproductive variation in North American turtles: Temperature, egg size and optimality. Zoology 115:160–169.

Rostal, D.C. 2014. Reproductive physiology of North American tortoises. Pp. 37–45 in Biology and Conservation of North American Tortoises (D. Rostal, E.D. McCoy and H.R. Mushinsky, eds.). Johns Hopkins University Press, USA.

Rostal, D.C., and D.N. Jones, Jr. 2002. Population biology of the Gopher Tortoise (*Gopherus polyphemus*) in southeast Georgia. Chelonian Conservation and Biology 4:479–487.

Rostal, D.C., V.A. Lance, J.S. Grumbles, and A.C. Alberts. 1994. Seasonal reproductive cycle of the Desert Tortoise (*Gopherus agassizii*) in the eastern Mojave Desert. Herpetological Monographs 8:72–82.

Rothermal, B.B., and T.D. Castellón. 2014. Factors affecting reproductive output and egg size in a southern population of Gopher Tortoises. Southeastern Naturalist 13:705–720.

Ryan, K.M., and P.V. Lindeman. 2007. Reproductive allometry in the Common Map Turtle, *Graptemys geographica*. American Midland Naturalist 158:49–59.

Sarkar, S., N.K. Sarkar, P. Das, and B.R. Maiti. 1996. Photothermal effects on ovarian growth and function in the soft-shelled turtle *Lissemys punctata punctata*. Journal of Experimental Zoology 274:41–55.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Seager, R., M. Ting, I. Held, . . . N. Naik. 2007. Model predictions of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184.

Sieg, A.E., M.M. Gambone, B.P. Wallace, S. Clusella-Trullas, J.R. Spotila, and H.W. Avery. 2015. Mojave desert tortoise (*Gopherus agassizii*) thermal ecology and reproductive success along a rainfall cline. Integrative Zoology 10:282–294.

Smith, C.S., and S.D. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499–506.

Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, USA.

Stephens, P.A., I.L. Boyd, J.M. McNamara, and A.I. Houston. 2009. Capital breeding and income breeding: Their meaning, measurement, and worth. Ecology 90:2057–2067.

Stitt, E.W. 2004. Demography, Reproduction, and Movements of Desert Tortoises (*Gopherus agassizii*) in the Rincon Mountains, Arizona. M.S. thesis, University of Arizona, USA.

Sullivan, B.K., R. Averill-Murray, K.O. Sullivan, J.R. Sullivan, E.A. Sullivan, and J.D. Riedle. 2014. Winter activity of the Sonoran Desert Tortoise (*Gopherus morafkai*) in central Arizona. Chelonian Conservation and Biology 13:114–119.

Turner, F.B., and D.C. Randall. 1989. Net production by shrubs and winter annuals in southern Nevada. Journal of Arid Environments 17:23–26.

Turner, F.B., P.A. Medica, and C.L. Lyons. 1984. Reproduction and survival of the desert tortoise (*Scaptochelys agassizii*) in Ivanpah Valley, California. Copeia 1984:811–820.

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 Company, USA.

Turner, R.M., and D.E. Brown. 1982. Sonoran desert scrub. Pp. 181–221 in Biotic Communities of the American Southwest-United States and Mexico: Desert Plants 4 (D. Brown, ed.). University of Arizona, Boyce Thompson Arboretum, USA.

[USFWS] U.S. Fish and Wildlife Service. 2016. Health assessment procedures for the desert tortoise (*Gopherus agassizii*): A handbook pertinent to translocation. U.S. Fish and Wildlife Service, Desert Tortoise Recovery Office, USA. Available at http://www.fws.gov/nevada/desert_tortoise/documents/reports/2016/may-2016-desert-tortoise-health-eval-handbook.pdf. Archived by WebCite at http://www.webcitation.org/6xzmVqkLG on 17 March 2018.

van de Pol, M., L.D. Bailey, N. McLean, L. Rijsdijk, C.R. Lawson, and L. Brouwer. 2016. Identifying the best climatic predictors in ecology and evolution. Methods in Ecology and Evolution 7:1246–1257.

Van Devender, T.R., R.C. Averill-Murray, T.C. Esque, P.A. Holm, V.M. Dickinson, C.R. Schwalbe, E.B. Wirt, and S.L. Barrett. 2002. Grasses, mallows, desert vine, and more: Diet of the Desert Tortoise in Arizona and Sonora. Pp. 159–193 in The Sonoran Desert Tortoise: Natural History, Biology, and Conservation (T.R. Van Devender, ed.). University of Arizona Press and Arizona-Sonora Desert Museum, USA.

van Riper, C., III, J.R. Hatten, J. T. Giemakowski, . . . C.R. Schwalbe. 2014. Projecting Climate Effects on Birds and Reptiles of the Southwestern United States. Open-File Report 2014-1050. U.S. Geological Survey, USA.

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.

Warner, D.A., D.A.W. Miller, A.M. Bronikowski, and F.J. Janzen. 2017. Decades of field data reveal that turtles senesce in the wild. Proceedings of the National Academy of Sciences 113:6502–6507.

Webb, W., S. Szarek, W. Lauenroth, R. Kinerson, and M. Smith. 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. Ecology 59:1239–1247.

Weber, S.B., J.D. Blount, B.J. Godley, M.J. Witt, and A.C. Broderick. 2011. Rate of egg maturation in marine turtles exhibits 'universal temperature dependence'. Journal of Animal Ecology 80:1034–1041.

Wirt, E.B., and P.A. Holm. 1997. Climatic Effects on Survival and Reproduction of the Desert Tortoise (*Gopherus agassizii*) in the Maricopa Mountains, Arizona. IIPAM Report I92035. Arizona Game and Fish Department, USA.

Zuur, A.F., E.N. Ieno, and G.M. Smith. 2007. Analysing Ecological Data. Springer, USA.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed Effects Models and Extensions in Ecology in R. Springer, USA.

Zylstra, E.R., R.J. Steidl, C.A. Jones, and R.C. Averill-Murray. 2013. Spatial and temporal variation in survival of a rare reptile: A 22-year study of Sonoran Desert Tortoises. Oecologia 173:107–116.

Accepted on 5 May 2018
Published on 8 October 2018

Appendix.—Reproductive sampling at Sugarloaf Mountain, Arizona: 1 indicates reproductive data (radiographic or ultrasonographic) are available for that year; 0 indicates that the tortoise was monitored, but reproductive output was inconclusive.

Tortoise no.	1993	1997	1998	1999	2000	2001	2002	2003	2004	2005	Count
Adults											
1	1	1	1	1	1[b]	1	1	1	1[b]	1[a]	10
3		1	1	1	1	1	1	1	1	1	9
4	1										1
12	1										1
13	1										1
14	1		1	1	1	1	1				6
17	1		1	1	1	1	1	1	1	1	9
18	1										1
19	1										1
21	1										1
25		1	1								2
29		1	1	1	1	1	0	1			6
33	1										1
46		1	1	1	1	1	1	0	0	1	7
51		1	1	1							3
55		1	1								2
57		1	1	1	1	1		0	1		6
58		1	1	1	1	1	1	0	1	0	7
63		1	1	1	1	1	1				6
65		1	1	1	1	0					4
66			1	1	1	1	1	1	1	1	8
67			1		1	1			1		4
68		1	1	1	1	1	1[a]	1	1	0	8
69					1	1					2
71				1	1						2
72					1	1	1	1	1	1	6
77			1[a]							0	1
80			1		1						2
81			1	1	1						3
86				1	1	1	1	1	1	1	7
625								1	0	0	1
Count	10	12	19	16	19	15	11	9	10	7	31
$\bar{X} \pm$ SD											3.8 ± 2.76
Subadults (CL < 220 mm)											
45						0	1	1	0		2
56			1	1	0	0	0	0	0		2
61		1	1	1							3
73			1	1	1	0	1	1	1		6
Count	0	1	3	3	1	0[c]	2	2[c]	1	0	4

[a] Clutch retained from previous year; not included in analyses.

[b] New eggs added to clutch retained from previous year; old clutch not included in analyses.

[c] One additional tortoise was found opportunistically and scanned ultrasonagraphically.