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Reproduction of *Gopherus agassizii* in the Sonoran Desert, Arizona

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ABSTRACT. – I studied reproduction of the desert tortoise, *Gopherus agassizii*, at a population in the Sonoran Desert in Arizona in 1993 and 1997–99. Females laid a single clutch of eggs near the onset of the summer rainy season, but not all females reproduced every year. Both winter and spring rainfall influenced clutch frequency. The smallest female to lay eggs was 220 mm midline carapace length, but minimum reproductive size was negatively correlated with winter rainfall. Mean clutch size ranged from 3.8 to 5.7 eggs and was not related to female body size or rainfall. Mean egg width was not related to year, rainfall, or clutch size, but large females laid larger eggs than did small females. Nest predation appeared to be high; some hatchlings emerged from nests during late summer, but hatchlings from clutches laid late in the year may overwinter in the nest. Data collected in 1997 from a second population were generally similar. Reproductive characteristics differ between tortoise populations in the Sonoran, eastern Mojave, and western Mojave deserts.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Gopherus agassizii*; tortoise; ecology; reproduction; life history; Sonoran Desert; Mojave Desert; USA; Arizona

The desert tortoise, *Gopherus agassizii*, has the broadest range of latitude and habitats of the four species of North American tortoises (Auffenberg and Franz, 1978; Patterson, 1982; Germano et al., 1994), but reproductive biology and ecology are known primarily from populations within the Mojave Desert (Hampton, 1981; Turner et al., 1984, 1986; Roberson et al., 1989; Rostal et al., 1994; Henen, 1994, 1997; Karl, 1998; Mueller et al., 1998; Wallis et al., 1999). Even though Mojave and Sonoran desert populations differ genetically (Lamb et al., 1989; Glenn et al., 1990), morphologically (Germano, 1993), and ecologically (Luckenbach, 1982), little is known about basic differences in life history, including geographic variation in reproduction across the species' range. Murray et al. (1996) summarized one year of reproductive output of *G. agassizii* from a population in the Sonoran Desert, Arizona. This study augments that work by providing three additional years of data from the same population, as well as one year of data from a second population in the Sonoran Desert. I also compare reproductive strategies among populations (Mojave and Sonoran) of the species.

METHODS

Study Area and Seasons. — My primary study site was near Sugarloaf Mountain on the Tonto National Forest, Maricopa County, Arizona, USA (33°41'N, 111°31'W). Elevations at Sugarloaf range from 549–853 m with steep, rocky slopes divided by many arroyos. Boulders up to 4 m diameter occur on many slopes. In 1997 I also sampled tortoises from a second site, about 100 km to the south in the Granite Hills, Pinal County, Arizona (32°50'N, 111°21'W). Elevations at Granite Hills range from 600–702 m, and topography is similar to Sugarloaf. Both sites are in the northeastern Sonoran Desert with vegetation classified in the paloverde-mixed cacti series of the Arizona Upland Subdivision (Turner and Brown, 1982).

I recorded rainfall each week from a rain gauge at Sugarloaf, and I summarized long-term (1939–99) rainfall data from the National Oceanic and Atmospheric Administration's nearest weather station, about 13 km to the south (Stewart Mountain; 33°34'N, 111°32'W, 433 m elevation). I summarized annual rainfall data according to three seasons defined by average environmental conditions and tortoise activity (Averill-Murray et al., 2002a). Summer included the months of July through October, containing the monsoon rainy season and peak tortoise activity. Winter (November through February) was usually also wet, but cool and with little tortoise activity. Spring (March through June) was generally characterized by increasing temperatures, decreasing rainfall, and variable tortoise activity.

Telemetry and Radiography. — Each year at Sugarloaf I monitored female tortoises (184–289 mm straight midline carapace length [CL]) weekly using radiotelemetry. I attached radiotransmitters (< 5% body weight; AVM Instrument Co., Telonics, or Wildlife Materials) to the anterior carapace using 5-minute gel epoxy (Devcon). I radiographed tortoises with an HF-80 (MinXray) portable X-ray machine powered by a gasoline generator. I placed tortoises upright on loaded film cassettes (high-speed cassettes refurbished by Custom X-Ray Imaging Services) at a constant "focus-to-film" distance of 61 cm. I used Custom X-Ray high-speed blue private practice film. X-ray exposure times ranged from 0.12–0.24 sec at 65 kVP, depending on tortoise size (CL). See Murray et al. (1996) for slight deviations in 1993 from the methods described above.

Radiographic sampling frequencies and sample sizes each year are given in Table 1. I also randomly sampled tortoises from the telemetered population in late summer 1997, spring 1998, summer 1998, and spring 1999 to deter-

Table 1. Radiographic sampling frequencies and sample sizes (*n*) each year at Sugarloaf. See text for measures taken to minimize handling and radiation exposure.

Year	*n*	Radiographic sampling
1993	10	Weekly, 12 June – 11 July, then biweekly through 12 September
1997	13	Weekly, 15 May – 12 August, then once each in mid-September and mid-October
1998	22	Biweekly, 21 May – 6 August
1999	20	Biweekly, 28 May – 23 July[a]

[a]Two tortoises that retained eggs longer than expected were periodically radiographed until as late as 2 October.

mine whether tortoises developed shelled eggs outside the radiography focal periods described in Table 1. Occasionally, I could not retrieve a randomly-selected tortoise from its burrow for radiography, so I simply selected the next tortoise on the list of random numbers. I assumed that those radiographed represented random samples of the population. In late summer 1997, I sampled 9 tortoises on 16 September and 8 tortoises on 21 October. In spring 1998, I sampled 10 tortoises on 1 April and 16 tortoises on 1 May. On 7 May, I radiographed 4 of the 6 tortoises not sampled plus 1 that was sampled on 1 May. In summer 1998, I radiographed 10 tortoises each on 14 August, 3 September, and 6 October. In spring 1999, I radiographed 8 tortoises on 1 April and 11 tortoises on 6 May; several tortoises that had not yet left hibernation in spring 1999 (5 and 2 on each date, respectively) were not sampled. I calculated the minimum overall probability that I would detect eggs in each season, if any female in the telemetered population actually had eggs, based on the samples of negative radiographs. I limited this analysis to tortoises ≥ 220 mm CL; tortoises below this size have not been observed to produce eggs at this site. First, I determined the maximum probability of each sample containing no gravid females (P_0), if at least 1 of the total number of telemetered females was gravid, based on the hypergeometric distribution:

$$P_0 = [(qn)!*(n-k)!]/[n!*(qn-k)!],$$

where **q** is the proportion of tortoises without eggs (set to [n-1]/n), ***n*** is the number of telemetered females, and **k** is the size of the random sample. The overall power of detecting a gravid female in a seasonal sample of tortoises was then 1 minus the product of each sample's P_0 within that season.

In all years, if I could detect eggs by palpation after I had confirmed clutch size on a previous radiograph, that tortoise was not radiographed during its normal rotation; this procedure allowed me to minimize handling, cumulative radiographic exposure, and stress to individual tortoises. For the same reasons, beginning in 1998 I provided tortoises that voided their bladders during processing an opportunity to rehydrate by placing them in a plastic container with water for several minutes before returning them to their capture location; containers were rinsed, disinfected with chlorhexidine diacetate (Nolvasan), and sun-dried between uses. In 1999 I processed 3 tortoises below the minimum reproductive size observed in the 3 prior years every third week instead of second, to reduce unnecessary handling and radiation exposure. Additionally, ultrasonographic analyses for 4 weeks during the 1999 season obviated unnecessary radiographic exposure to tortoises without eggs (B.T. Henen and R.C. Averill Murray, unpubl. data).

Table 2. Seasonal rainfall (mm) at Sugarloaf and Stewart Mountain, Arizona. Winter = November–February; Spring = March–June; Summer = July–October. * = rainfall significantly above average (z residual = 2.976).

	Sugarloaf			Stewart Mountain		
Year	Winter	Spring	Summer	Winter	Spring	Summer
1992	—	96.1[a]	221.2	224.0	131.1	186.2
1993	367.0	92.6	—	413.8*	74.9	83.3
1996	—	0.0[a]	68.6	82.8	16.0	72.9
1997	76.5	50.5	83.3	102.9	13.5	61.7
1998	252.4	74.1	96.1	257.8	78.2	115.3
1999	72.1	61.2	128.6	74.2	33.8	126.8
Mean	192.0	62.4	119.6	192.6	57.9	107.7
(SD)	(143.7)	(35.3)	(61.0)	(132.9)	(45.5)	(45.8)
1939–99				136.9	48.9	123.5
(SD)				(82.4)	(39.0)	(61.7)

[a]Totals include only April–June.

Tortoises at Granite Hills were individually marked but not telemetered, so field technicians searched for as many females as possible during one evening and morning survey each week in 1997. I radiographed a total of 16 females up to 5 times each at Granite Hills from 4 June to 14 August.

I determined clutch size directly from radiographs and measured egg-width images with calipers (to 0.05 mm) and corrected for magnification (Graham and Petokas, 1989). I estimated the "egg-to-film" distance for this correction to be 30 mm (Wallis et al., 1999). I estimated oviposition date for each gravid tortoise as the midpoint between the date eggs were last recorded by radiography, palpation, or ultrasonography and the first date on which eggs were no longer present in the tortoise.

Statistical Analysis. — Seasonal rainfall at Sugarloaf and Stewart Mountain were correlated (Table 2; $r^2 = 0.941$, $t_{15} = 14.41$, $p < 0.001$), so I evaluated whether seasonal rainfall deviated from the long-term (1939–99) norm by analyzing residuals. I square-root-transformed the Stewart Mountain data to achieve normality, then considered seasonal rainfall for a given year to be significantly abnormal if the absolute value of its standardized residual was > 1.96.

I examined reproductive patterns with analysis of covariance (ANCOVA), controlling for CL. I did not use partial repeated measures analyses, because only 6 of 21 egg-laying individuals reproduced in more than one year. I examined the effects of seasonal rainfall on mean annual reproductive parameters with simple linear regression (Sokal and Rohlf, 1995). I also described significant body-size relationships revealed by ANCOVA with simple linear regression. I examined non-predictive relationships with simple linear

Table 3. Reproduction of female desert tortoises (≥ 220 mm CL) at Sugarloaf Mountain, 1993 and 1997–99. Number of telemetered females given in column headings. Ranges for oviposition date, mean CL, clutch size, and mean egg width given in parentheses, sample sizes in brackets.

	1993 (n = 10)	1997 (n = 11)	1998 (n = 19)[a]	1999 (n = 16)
Eggs first visible	<12 Jun[b]	31 May ± 6 d (28 May–10 Jun)	17 Jun ± 9 d (4 Jun–1 Jul)	19 Jun ± 11 d (28 May–2 Jul)
Egg layers	8	4	13	7
Clutch frequency	0.80 ± 0.13	0.36 ± 0.15	0.68 ± 0.11	0.44 ± 0.13
Oviposition date	27 Jun ± 14 d (9 Jun–25 Jul) [8]	1 Jul ± 7 d (20 Jun–4 Jul) [4]	13 Jul ± 9 d (12 Jun–3 Aug) [12]	25 Jul ± 21 d (9 Jul–30 Aug) [5][c]
Mean CL (mm)	247 ± 12.9 (220-260) [8]	253 ± 11.5 (239-267) [4]	248 ± 16.0 (229-287) [13]	260 ± 16.8 (239-289) [7]
Clutch size	5.7 ± 2.43 (3-9) [7][d]	3.8 ± 1.26 (2-5) [4]	5.7 ± 1.49 (4-9) [13]	4.6 ± 1.51 (3-7) [7]
Egg width (mm)	35.7 ± 1.74 (32.1-37.7) [7][d]	34.9 ± 1.18 (33.5-36.4) [4]	35.4 ± 1.72 (32.8-39.7) [13]	36.2 ± 2.12 (33.8-39.6) [7]

[a]Excludes 1 clutch presumably retained from the previous year but includes data from an untelemetered female (except for eggs first visible and oviposition date).
[b]Radiography initiated on 12 June, after eggs had shelled.
[c]Excludes 1 clutch retained over winter and 1 tortoise lost prior to oviposition.
[d]Excludes 1 clutch laid prior to initiation of radiography (Murray et al., 1996).

correlation. I conducted analyses with SYSTAT 8.0 (SPSS, 1998), considered results significant at $p < 0.05$, and report all means ± 1 standard deviation (SD; binomial for clutch frequency).

RESULTS

Rainfall. — Residual analysis of Stewart Mountain rainfall since 1939 revealed that seasonal rainfall was abnormally high during spring 1941, winter 1979, and winter 1993, and abnormally low during spring 1947, 1955, and 1959, winter 1961, and winter and spring 1972 (|z residuals| > 1.96). Even though rainfall varied substantially during the study, the extremely wet winter of 1993 was the only statistically significant deviation from average (Table 2).

Egg Development. — Few tortoises at Sugarloaf had oviductal (shelled) eggs before June or after August. Eggs were first visible on radiographs from late May to early July (Table 3). Samples of negative radiographs resulted in a ≥ 88% chance of detecting eggs in our spring and late summer samples, if any tortoise in the telemetered population was actually gravid (Table 4). The April 1998 radiography sample revealed no gravid tortoises, but one tortoise (#77) was found with a single egg on 1 May. The 7 May sample resulted in no additional gravid females. I had 94% probability of detecting eggs in spring 1998, if any tortoise (other than #77) was gravid. Although tortoise #77 was not telemetered during the 1997 reproductive season, I believe its single egg was retained from 1997. I excluded this observation from all analyses based on the following evidence. First, tortoise #77 laid this egg on approximately 12 June, while clutches from all other tortoises that reproduced that year did not even appear on radiographs until 4–26 June. Second, 1997 was a dry year (below average; Table 2), during which most females did not reproduce and those that did had small clutch sizes (see below). Most tortoises did reproduce in 1998, and mean clutch size increased (see below); tortoise #77's clutch of 1 egg in 1998 does not fit this pattern.

Clutch Frequency and Oviposition. — Mean clutch frequency ranged from 0.36 to 0.80 each year (Table 3). No tortoise laid more than 1 clutch in a year. Female tortoises generally laid eggs near the beginning of the summer monsoon season, which usually occurs in early July, but mean oviposition occurred later during each year of the study (Table 3; $F_{3,24} = 4.94$, $p = 0.008$). Oviposition dates also varied by CL ($F_{1,24} = 4.65$, $p = 0.041$), with larger females tending to lay later than smaller females (r = 0.440, combined years). However, this relationship was influenced by a single outlier; exclusion of the most extreme point eliminated the significant relationship ($F_{1,23} = 1.00$, $p = 0.329$). Mean oviposition date was not correlated with prior summer, winter, or spring rainfall ($p \geq 0.478$).

Both winter (r = 0.983, $t_4 = 7.58$, $p = 0.017$) and spring (r = 0.975, $t_4 = 6.23$, $p = 0.025$) rainfall influenced mean clutch frequency (Fig. 1). Correlation between these seasonal measures of rainfall was high, though not statistically significant, during the 4 years of the study (r = 0.932, p = 0.068). Prior summer rainfall did not affect clutch frequency (r = 0.781, $t_4 = 1.77$, $p = 0.219$).

Body Size. — Reproductive females averaged 247 (± 12.9) mm CL in 1993 to 260 (± 16.8) mm in 1999 (Table 3). The smallest reproductive female in a year ranged from 220

Table 4. Probability of detecting eggs in seasonal radiography of desert tortoises (≥ 220 mm CL) at Sugarloaf, 1997–99. n = number of telemetered females, N = number of radiography sample sessions per season, k = radiograph sample size for each N.

Season	n	N	k	Probability
Late summer 1997 (Sep–Oct)	11	2	9, 8	95%
Spring 1998[a] (Apr–May)	17	2	8, 15	94%
Summer 1998 (Aug–Oct)	18	3	10, 10, 10	91%
Spring 1999 (Apr–May)	15	2	8, 11	88%

[a]Excludes 1 clutch retained from 1997 (see text).

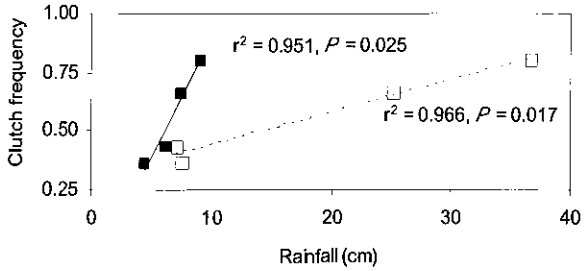

Figure 1. Clutch frequency vs. seasonal rainfall for Sugarloaf desert tortoises. Winter (□) = November–February; Spring (■) = March–April. Clutch frequency = 0.301 + 0.14(winter rain, cm). Clutch frequency = 1.00(spring rain, cm) - 0.104.

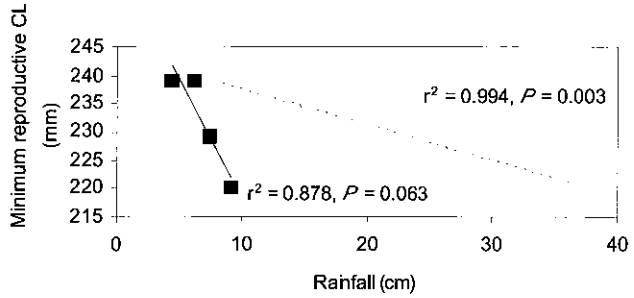

Figure 2. Minimum size of reproductive female desert tortoises vs. seasonal rainfall at Sugarloaf. Winter (--) = November–February; Spring (■) = March–April.

mm CL in 1993 to 239 mm in both 1997 and 1999 (Table 3). Mean body size of reproductive females was not significantly correlated with seasonal rainfall ($p \geq 0.146$), but minimum reproductive size was negatively correlated with winter rainfall ($r = -0.997$, $p = 0.003$; Fig. 2), nearly so with spring rainfall ($r = -0.937$, $p = 0.063$; Fig. 2), and not with prior summer rainfall ($p = 0.152$). Annual minimum reproductive size and mean clutch frequency were negatively correlated ($r = -0.977$, $p = 0.023$).

Clutch and Egg Size. — Mean clutch size ranged from 3.8 (± 1.26) eggs in 1997 to 5.7 eggs in both 1993 (± 2.43 eggs) and 1998 (± 1.49) (Table 3). There was no relationship between clutch size and year ($F_{3,31} = 2.12$, $p = 0.122$) or female body size ($F_{1,31} = 1.05$, $p = 0.315$; Fig. 3). Spring rainfall appeared to be highly correlated with mean clutch size ($r = 0.937$), but the relationship was not statistically significant ($t_4 = 3.80$, $p = 0.063$), probably due to the small sample size. Likewise, mean clutch size did not vary significantly with winter ($t_4 = 2.62$, $p = 0.120$) or summer rainfall ($t_4 = 1.04$, $p = 0.408$). However, increased summer rainfall appeared to result in increased variability (standard deviation) in clutch size ($r = 0.995$, $t_4 = 13.92$, $p = 0.005$).

Mean egg width ranged from 34.9 (± 1.18) mm in 1997 to 36.2 (± 2.12) mm in 1999 (Table 3), up to 4% variation among years. Individual females' mean egg width was not related to year ($F_{3,31} = 1.00$, $p = 0.410$), but larger females laid larger eggs than smaller females ($F_{1,26} = 24.64$, $p < 0.001$; $r = 0.680$; Fig. 3). Egg width was not correlated with clutch size ($p = 0.081$), and variation in seasonal rainfall also did not influence mean egg width ($r \leq 0.402$, $t_4 \leq 0.62$, $p \geq 0.598$).

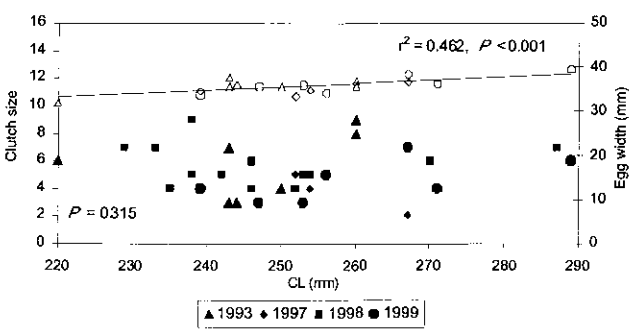

Figure 3. Clutch size (closed symbols) and mean egg widths (open symbols) vs. midline carapace length (CL) for Sugarloaf desert tortoises. Mean egg width (mm) = 16.504 + 0.076(CL, mm).

Nests. — In 1997 and 1998, I attempted to find and monitor as many nests at Sugarloaf as possible. I found only nests laid inside burrow entrances. Of 4 nests laid in 1997, 3 appeared to have been destroyed by predators; 1 (which was never found) had an unknown outcome. Of the 13 clutches laid in 1998, I confirmed 4 nests inside burrows and suspected 2 others based on the females' occupation of the same burrows for several weeks after ovipositing (Murray et al., 1996); I was unable to find the remaining 7 nests. Of the 4 confirmed nests, 2 appeared to have been destroyed by predators and 2 appeared to have successfully hatched. I observed 2 hatchlings in one of these nests on three visits between 15 and 29 October 1998. The last hatchling (43.5 mm CL, 16 g) exited the nest on 29 October.

Granite Hills. — Of 16 females radiographed at Granite Hills in 1997 (CL ranged from 172–249 mm), 4 (226–249 mm CL, $\bar{x} = 236 \pm 10.6$ mm) were gravid. Since these tortoises were not telemetered and I was unable to locate the same tortoises each week, I did not estimate clutch frequency. Oviposition would have occurred as early as late June to early August, based on dates on which eggs were visible on radiographs (4 June – 7 August). Clutch size ($\bar{x} = 3.3 \pm 2.06$ eggs) was unrelated to female body size ($r = 0.077$, $t_4 = 0.11$, $p = 0.923$), and mean egg width ($\bar{x} = 32.4 \pm 2.01$ mm) was unrelated to clutch size ($p = 0.427$). Female body size appeared to influence mean egg size ($r = 0.824$), but not significantly so for this small sample ($t_4 = 2.06$, $p = 0.176$).

DISCUSSION

Virtually nothing is known about reproduction in *Gopherus agassizii* in the southern half of its range in Mexico (Germano, 1994a), as its habitat grades from the Sonoran Desert through Sinaloan thornscrub and into Sinaloan deciduous forest (Germano et al., 1994). Reproductive output is highly variable throughout the southwestern U.S., however, both within and between populations. Individual variation within the unpredictable environments of the Mojave and Sonoran deserts may obscure underlying reproductive patterns and life history characteristics (see Gibbons and Greene, 1990), but this study reinforces conclusions derived from previous Mojave Desert studies. It also suggests important intraspecific differences in life history between the tortoises inhabiting the two deserts.

Winter rainfall and subsequent spring annual plant production can influence mean clutch frequency (Turner et al., 1986) and annual egg production (Henen, 1994, 1997) in the Mojave Desert through the nutrients available in forage. However, simple correlations between environmental condition and reproductive output do not always occur (Karl, 1998; Mueller et al., 1998). Reproductive output reaches asymptotic levels and may be constrained by other factors, such as body size and maternal nutrient reserves, especially when spring forage is abundant (Henen, 1997; Wallis et al., 1999). Mojave females typically lay 1–2 clutches (occasionally 3) each year (Turner et al., 1986; Henen, 1994, 1997; Karl, 1998; Mueller et al., 1998; Wallis et al., 1999); most lay at least some eggs even following dry winters by sacrificing nutrient reserves and body condition (Henen, 1997). Reserves that are expended for reproduction may also affect energy available for egg production the next year (Henen, 1997).

No tortoise laid more than a single clutch during any year of the current study, and most skipped reproduction completely during at least one year. In 1993, 20% of the females even skipped reproduction (Table 3) after one of the wettest winters on record (Table 2) and the resultant burst of spring vegetation (*pers. obs.*). Clutch frequency (effectively the proportion of females reproducing in a year) was correlated with both prior winter and spring rainfall (and presumably subsequent plant production; Turner and Randall, 1989). Neither clutch size nor egg size was clearly related to seasonal rainfall; 61% greater winter rainfall in 1993 compared to above-average winter rainfall in 1998 (Table 2) resulted in the same mean clutch size in both years (Table 3). However, a marginally non-significant correlation suggests that wet springs with abundant forage seem to enable reproductive females to produce larger clutches than during drier years. As described for Mojave tortoises above, other constraints probably limited reproductive output in the extraordinarily wet 1998.

Summer is the peak rainy and tortoise activity season of the year in the Sonoran Desert (Averill-Murray et al., 2002a), but rather than contributing to an increase in mean clutch size, increasing summer rainfall resulted in more variable clutch sizes. Winter/spring rainfall may have direct effects on some aspects of reproductive output of Sonoran Desert tortoises through forage production during egg development, while the prior year's summer rainfall and plant production may affect the recovery of maternal nutrient reserves and hydration status after egg-laying. Ongoing study should help resolve relative contributions of seasonal rainfall and plant production to reproductive output, as sample sizes and environmental variation increase.

Maternal body size of *G. agassizii* in the Mojave Desert affects reproductive output in various ways (Henen, 1994), including clutch frequency (Turner et al., 1986; Karl, 1998; Wallis et al., 1999), clutch size (Turner et al., 1986; Karl, 1998; Mueller et al., 1998; Wallis et al., 1999), annual egg production (Karl, 1998; Mueller et al., 1998; Wallis et al., 1999), and egg size and clutch volume (Wallis et al., 1999). Interestingly, Wallis et al. (1999) found that the size of the first clutch, but not the second, was correlated with body size, while Karl (1998) found the opposite pattern. Physical constraints of a female turtle's shell limit the maximum number of eggs she can carry (Congdon and Gibbons, 1987), but female size usually explains very little variation in clutch size within populations (Wilbur and Morin, 1988; see Turner et al., 1986; Karl, 1998; Mueller et al., 1998; Wallis et al., 1999). I found no relationship between body size and clutch size in this study. Female size affected clutch frequency at Sugarloaf in that smaller tortoises failed to produce eggs following dry seasons, but still not all large females reproduced every year. Larger females did lay larger eggs, though there was still > 50% unexplained variation.

Ovarian follicles of *G. agassizii* in the Mojave Desert mature to near-ovulatory size prior to hibernation (Rostal et al., 1994; Henen and Oftedal, 1998). Thus, Mojave females emerge from hibernation almost ready to lay eggs. Smaller tortoises tend to lay their clutches later in the spring than larger tortoises, probably because small tortoises have relatively less nutrient reserves, relying more on spring forage to obtain energy for egg production (Wallis et al., 1999). Large females may benefit by having greater reserves to produce eggs shortly after emerging from hibernation and then still have time during the nesting season to lay a second or third clutch, at least during favorable conditions. Ovarian follicles do not mature until after hibernation at Sugarloaf (B.T. Henen, R.C. Averill-Murray, and T. Christopher, unpubl. data), and ovulation does not typically occur until May or June when Mojave tortoises are already laying their first or second clutches (Turner et al., 1986; Karl, 1998; Mueller et al., 1998; Wallis et al., 1999). Oviposition at the Sonoran Desert sites typically occurred near the onset of the summer rainy season, from June through August, so all females had the opportunity to forage during the spring before laying eggs. Late oviposition dates at Sugarloaf in 1998 and 1999 suggest that some eggs or hatchlings may overwinter in the nest before hatching/emerging.

Derived Mojave Characteristics. — The fossil record suggests that *G. agassizii* evolved in a more mesic climate, and the formation of the Sonoran and Mojave deserts during Miocene to Pleistocene glacial climates left tortoises in an increasingly dry and unpredictable environment (Van Devender, 2002). Mean winter rainfall values broadly overlap between the Mojave and Sonoran deserts, but summer rainfall decreases from the Sonoran Desert, through the eastern Mojave, to the extremely dry western Mojave (Turner, 1982; Turner and Brown, 1982; Germano, 1994b; Henen et al., 1998; Wallis et al., 1999). If we assume that Sonoran tortoises are most similar to the ancestral *G. agassizii* stock, we can form hypotheses for the evolution of derived reproductive traits in Mojave tortoises.

Females as small as 220 mm CL produced eggs in this study. The minimum recorded size at first reproduction in the western Mojave Desert (WMD) is 176 mm CL (Germano, 1994a) and 180 mm in the eastern Mojave (EMD; Karl, 1998). Though precise data on growth are lacking across the range of the desert tortoise, Mojave tortoises also appear to

mature at earlier ages than Sonoran tortoises (Germano, 1994a). Adult survival appears to be similar between the two deserts (U.S. Fish and Wildlife Service, 1994; Howland and Klug, 1996; Averill-Murray et al., 2002b), but the small size of hatchlings and juveniles might predispose them to lower average survival under the harsher conditions of the Mojave Desert. Therefore, earlier maturation and production of offspring in Mojave tortoises might balance higher juvenile mortality compared to Sonoran tortoises (see Stearns, 1992:123).

Sonoran tortoises invest their entire reproductive output in a single clutch during the relatively predictable summer rainy season and typically produce fewer eggs overall than in the Mojave Desert, except under extreme drought conditions. Annual egg production ranged from only 3.3 to 5.7 eggs/female at the Sonoran sites, compared to 4.9 (in a drought year) to 8.4 in the EMD (Karl, 1998; Wallis et al., 1999) and 3.0–3.6 (in drought years) to 7.0–7.1 in the WMD (Henen, 1994, 1997; Wallis et al., 1999). These differences may be an evolutionary product of greater hatchling survival in the Sonoran Desert than in the Mojave Desert. Limited data from this study suggest a high rate of nest predation, but no data exist on hatchling survival in the Sonoran Desert. Drier summer conditions in the Mojave Desert, especially in the WMD (Peterson, 1996; Henen et al., 1998; Wallis et al., 1998), may have resulted in tortoises adaptively producing a second and sometimes third clutch, thus maximizing the chance that at least some hatchlings will emerge coincident with favorable conditions. If this is true, hatchling cohorts from the same year, but from different clutches emerging under different environmental conditions, should exhibit different average survival rates.

Tortoises in the EMD produce relatively smaller eggs, produce more eggs overall, and lay their second clutches earlier than tortoises in the WMD (Wallis et al., 1999). Tortoises in the Sonoran Desert produce even smaller eggs relative to their body size than in the EMD (Fig. 4). Increasing relative egg size through an increasingly dry summer climate (Sonoran Desert to EMD to WMD), may be reproductively prudent, because eggs in the eastern and western Mojave Desert are more likely to hatch during unfavorable conditions than in the Sonoran Desert (Murray et al., 1996; Wallis et al., 1999). Hatchlings emerging in the Sonoran Desert have a relatively predictable supply of forage from which they can supplement their nutrient reserves to survive their first winter. Hatchlings in the EMD, with less predictable summer rains and flora, may benefit from increased parental investment (i.e., females produce larger eggs). Finally, hatchlings in the WMD experience a predictable lack of summer rain and flora, so still greater parental investment may provide nutrient reserves necessary to survive a harsh summer and the following winter. Late-hatching tortoises in the WMD, compared to the EMD, could also better conserve their larger nutrient reserves for surviving through winter (Wallis et al., 1999).

This reproductive pattern is consistent with the evolutionary trade-off between offspring size and number; the

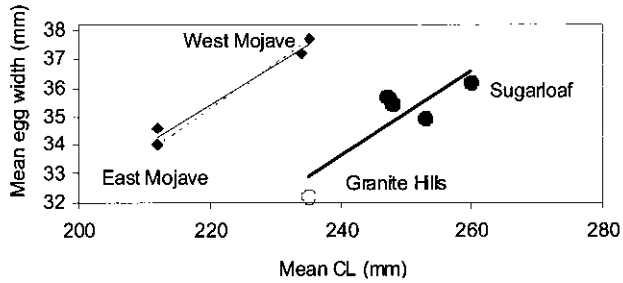

Figure 4. Mean egg width vs. mean midline carapace length (CL) for Mojave and Sonoran desert tortoises. Mojave Desert data are from 2 populations, 1992–93 (Wallis et al., 1999). Trend lines are for Mojave clutch 1 (solid) and Mojave clutch 2 (dashed) for combined years and 1997 clutches for Sonoran sites (Sugarloaf and Granite Hills).

trade-off between number and size of young should be at evolutionary equilibrium when the gain in parental fitness by adding one more offspring is less than the overall decrease in fitness due to lowered success of each individual offspring that results from lower investment per offspring (Stearns, 1992). Evolutionarily, Mojave females capitalized on relatively predictable winter rainfall and spring forage to increase their fitness in an increasingly unfavorable summer-rainfall environment by increasing both the size and number of their offspring. Through the Cenozoic drying of the WMD climate (Van Devender, 2002), larger egg (and presumably hatchling) size may have become adaptive to survive drier summers relative to those in the EMD (e.g., Morafka, 1994), while possibly balanced by slightly reduced clutch size.

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LITERATURE CITED

AUFFENBERG, W. AND FRANZ, R. 1978. *Gopherus agassizii*. Cat. Amer. Amphib. Rept. 212.1-2.

AVERILL-MURRAY, R.C., MARTIN, B.E., BAILEY, S.J., AND WIRT, E.B. 2002a. Activity and behavior of the Sonoran desert tortoise in Arizona. In: T.R. Van Devender (Ed.). The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. Tucson: Univ.

Arizona Press and Arizona-Sonora Desert Museum, pp. 135-158.

AVERILL-MURRAY, R.C., WOODMAN, A.P., AND HOWLAND, J.M. 2002b. Population ecology of the Sonoran desert tortoise in Arizona. In: Van Devender, T.R. (Ed.). The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. Tucson: Univ. Arizona Press and Arizona-Sonora Desert Museum, pp. 109-134.

CONGDON, J.D. AND GIBBONS, J.W. 1987. Morphological constraint on egg size: a challenge to optimal egg size theory? Proc. Nat. Acad. Sci. 84:4145-4147.

GERMANO, D.J. 1993. Shell morphology of North American tortoises. Am. Midl. Nat. 129:319-335.

GERMANO, D.J. 1994a. Growth and age at maturity of North American tortoises in relation to regional climates. Can. J. Zool. 72:918-931.

GERMANO, D.J. 1994b. Comparative life histories of North American tortoises. In: Bury, R.B., and Germano, D.J. (Eds.). Biology of North American Tortoises. Washington, D.C.: National Biological Survey, Fish and Wildlife Research 13, pp. 175-185.

GERMANO, D.J., BURY, R.B., ESQUE, T.C., FRITTS, T.H., AND MEDICA, P.A. 1994. Range and habitats of the desert tortoise. In: Bury, R.B., and Germano, D.J. (Eds.). Biology of North American Tortoises. Washington, D.C.: National Biological Survey, Fish and Wildlife Research 13, pp. 73-84.

GIBBONS, J.W. AND GREENE, J.L. 1990. Reproduction in the slider and other species of turtles. In: Gibbons, J.W. (Ed.). The Life History and Ecology of the Slider Turtle. Washington, DC: Smithsonian Inst. Press, pp. 124-137.

GLENN, J.L., STRAIGHT, R.C., AND SITES, J.W., JR. 1990. A plasma protein marker for population genetic studies of the desert tortoise (*Xerobates agassizi*). Great Basin Naturalist 50:1-8.

GRAHAM, T.E. AND PETOKAS, P.J. 1989. Correcting for magnification when taking measurements directly from radiographs. Herpetol. Rev. 20:46-47.

HAMPTON, A.M. 1981. Field studies of natality in the desert tortoise, *Gopherus agassizi*. Proc. Desert Tortoise Counc. Symp. 1981:128-138.

HENEN, B.T. 1994. Seasonal and annual energy and water budgets of female desert tortoises (*Xerobates agassizii*) at Goffs, California. Ph.D. Thesis, Univ. California, Los Angeles.

HENEN, B.T. 1997. Seasonal and annual energy budgets of female desert tortoises (*Gopherus agassizii*). Ecology 78:283-296.

HENEN, B.T. AND OFTEDAL, O.T. 1998. The importance of dietary nitrogen to the reproductive output of female desert tortoises (*Gopherus agassizii*). Proc. Second Comp. Nutrition Soc. Symp. 1998:83-88.

HENEN, B.T., PETERSON, C.C., WALLACE, I.R., BERRY, K.H., AND NAGY, K.A. 1998. Effects of climatic variation on field metabolism and water relations of desert tortoises. Oecologia 117:365-373.

HOWLAND, J.M. AND KLUG, C.M. 1996. Results of five consecutive years of population monitoring at three Sonoran Desert tortoise plots. Proc. Desert Tortoise Counc. Symp. 1995:74-87.

KARL, A.E. 1998. Reproductive strategies, growth patterns, and survivorship of a long-lived herbivore inhabiting a temporally variable environment. Ph.D. Thesis, Univ. California, Davis.

LAMB, T., AVISE, J.C., AND GIBBONS, J.W. 1989. Phylogeographic patterns in mitochondrial DNA of the desert tortoise (*Xerobates agassizi*), and evolutionary relationships among the North American gopher tortoises. Evolution 43:76-87.

LUCKENBACH, R.A. 1982. Ecology and management of the desert tortoise (*Gopherus agassizii*) in California. In: Bury, R.B. (Ed.). North American Tortoises: Conservation and Ecology. Washington, DC: U.S. Fish and Wildlife Service, Wildlife Research Report 12, pp. 1-38.

MORAFKA, D.J. 1994. Neonates: missing links in the life histories of North American tortoises. In: Bury, R.B. and Germano, D.J. (Eds.). Biology of North American Tortoises. Washington, DC: National Biological Survey, Fish and Wildlife Research 13, pp. 161-173.

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

MURRAY, R.C., SCHWALBE, C.R., BAILEY, S.J., CUNEO, S.P., AND HART, S.D. 1996. Reproduction in a population of the desert tortoise, *Gopherus agassizii*, in the Sonoran Desert. Herpetol. Nat. Hist. 4(1):83-88.

PATTERSON, R. 1982. The distribution of the desert tortoise (*Gopherus agassizii*). In: Bury, R.B. (Ed.). North American Tortoises: Conservation and Ecology. Washington, DC: U.S. Fish and Wildlife Service, Wildlife Research Report 12, pp. 51-55.

PETERSON, C.C. 1996. Anhomeostasis: seasonal water and solute relations in two populations of the desert tortoise (*Gopherus agassizii*) during chronic drought. Physiol. Zool. 69:1324-1358.

ROBERSON, J.B., BURGE, B.L., AND HAYDEN, P. 1989. Nesting observations of free-living desert tortoises (*Gopherus agassizii*) and hatching success of eggs protected from predators. Proc. Desert Tortoise Counc. Symp. 1985:91-99.

ROSTAL, D.C., LANCE, V.A., GRUMBLES, J.S., AND ALBERTS, A.C. 1994. Seasonal reproductive cycle of the desert tortoise (*Gopherus agassizii*) in the eastern Mojave Desert. Herpetol. Monogr. 8:72-82.

SOKAL, R.R. AND ROHLF, F.J. 1995. Biometry. New York: Freeman and Company, 887 pp.

SPSS. 1998. SYSTAT 8.0 [Computer program manual]. Chicago.

STEARNS, S.C. 1992. The Evolution of Life Histories. Oxford: Oxford Univ. Press, 249 pp.

TURNER, F.B., AND RANDALL, D.C. 1989. Net production by shrubs and winter annuals in southern Nevada. J. Arid Environ. 17:23-36.

TURNER, F.B., MEDICA, P.A., AND LYONS, C.L. 1984. Reproduction and survival of the desert tortoise (*Scaptochelys agassizii*) in Ivanpah Valley, California. Copeia 1984:811-820.

TURNER, F.B., HAYDEN, P., BURGE, B.L., AND ROBERSON, J.B. 1986. Egg production by the desert tortoise (*Gopherus agassizii*) in California. Herpetologica 42:93-104.

TURNER, R.M. 1982. Mohave desertscrub. In: Brown, D. (Ed.). Biotic Communities of the American Southwest-United States and Mexico. Desert Plants 4:157-168.

TURNER, R.M. AND BROWN, D.E. 1982. Sonoran desertscrub. In: Brown, D. (Ed.). Biotic Communities of the American Southwest-United States and Mexico. Desert Plants 4:181-221.

U.S. FISH AND WILDLIFE SERVICE. 1994. Desert tortoise (Mojave population) recovery plan. Portland, Oregon: U.S. Fish and Wildlife Service, 73 pp.

VAN DEVENDER, T.R. 2002. Cenozoic environments and the evolution of the gopher tortoises (Genus *Gopherus*). In: Van Devender, T.R. (Ed.). The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. Tucson: Univ. Arizona Press and Arizona-Sonora Desert Museum, pp. 29-51.

WALLIS, I.R., HENEN, B.T., AND NAGY, K.A. 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. J. Herpetol. 33:394-408.

WILBUR, H.M. AND MORIN, P.J. 1988. Life history evolution in turtles. In: Gans, C. and Huey, R.B. (Eds.). Biology of the Reptilia, Vol. 16, Ecology B, Defense and Life History. New York, Alan R. Liss, Inc., pp. 387-439.

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