SIZE STRUCTURE AND REPRODUCTION OF A POPULATION OF BLUNT-NOSED LEOPARD LIZARDS IN MID-ELEVATION BAJADA HABITAT

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Abstract.—In some species of lizards, differences in elevation affect population characteristics. The Blunt-nosed Leopard Lizard (*Gambelia sila*), a federally and state-listed Endangered species, occurs at elevations from 30–740 m, but is lacking in adequate elevational comparisons. From 1997 to 2006, I marked and recaptured 361 *G. sila*, including 119 adult male, 95 adult female, 25 juvenile male, and 25 juvenile female individuals, on the Lokern Natural Area, Kern County, California, USA, which is a mid-elevation habitat for this endangered species. I found that males differed significantly in average and upper decile size from females, although the largest males were 123 mm snout-vent length (SVL) and the largest females were 121 mm SVL. Adult *G. sila* generally became active in April and activity remained relatively high into July with some adults remaining above ground to the end of August. Gravid females were found as early as mid-April and as late as early August; average clutch size was 3.4 eggs. I made comparisons of body size, activity, and clutch size to other populations studies conducted at low-elevation valley floor sites and one study at a high-elevation site. There were no major differences in the population biology of *G. sila* among sites. Activity of lizards among sites was similar, but body size was generally greater at my mid-elevation site than the high-elevation and valley floor sites. Clutch size at my site also was greater than that at valley floor sites. More comprehensive studies of this species are needed for valley floor populations.

Key Words.-activity; clutch size; eggs; elevation effects; Gambelia sila; mass; snout-vent length

Introduction

The Blunt-nosed Leopard Lizard (Gambelia sila; Fig. 1) is a state and federally listed Endangered species (U.S. Fish and Wildlife Service [USFWS] 1998, 2010), mainly due to habitat loss on the floor of the San Joaquin Valley and adjacent valleys (Germano and Williams 1992a; Jennings 1995; USFWS 1998). Gambelia sila inhabit relatively flat, sparsely vegetated areas of the San Joaquin Desert (Germano et al. 2011) including the valley floor, Carrizo Plain, Elkhorn Plain, Cuyama Valley, and surrounding foothills (Montanucci 1965; Germano and Williams 1992a; USFWS 1998). The species ranges from 30-740 m elevation in desert habitats of alkali sink scrub, saltbush (Atriplex spp.) scrub, and non-native grasslands on the valley floor, and in saltbush scrub, Ephedra scrub, and non-native grasslands in surrounding foothill and higher elevation areas (Montanucci 1965; Stebbins 2003). This range of elevation can cause significant variation in demographic characteristics in lizard populations because of differences in biotic and abiotic factors. In some lizards, elevation has been shown to affect growth (Smith et al. 1994; Tracy 1999; Olsson and Shine 2002; Iraeta et al. 2006), body size (Tracy 1999; Ramírez-Bautista et al. 2021; Sheridan et al. 2022), survivorship (Ballinger 1979), life span (Comas et al. 2020), and reproductive traits (Iraeta et al. 2006; Morrissey et al. 2020; Ramirez-Bautista et al. 2021). It is important to the conservation of species that are endangered, such as *G. sila*, to understand if there are significant demographic differences among



FIGURE 1. Male Blunt-nosed Leopard Lizards (*Gambelia sila*) on the Lokern Natural Area, Kern County, California, USA, July 2003. Note the radio-telemetry collar attached to the lizard for a separate study. (Photographed by David Germano).

populations at different elevations and to quantify these differences.

Gambelia sila are the largest lizards in the San Joaquin Desert and males are larger than females (Montanucci 1965; Tollestrup 1982; Germano and Williams 2005). Similar to many desert lizards, G. sila are mostly insectivorous although they occasionally consume small lizards (Montanucci 1965, 1967; Tollestrup 1979; Germano et al. 2007), including their own young (Montanucci 1965; Germano and Williams 1994). Males are territorial (Montanucci 1965; Tollestrup 1983) and males and females obtain breeding colors by May and mate a number of times until the end of June (Montanucci 1965, 1970; Tollestrup 1982; Germano and Williams 2007). Activity typically begins in April and most adult activity ends in July, although a few adults can be found in August and September (Montanucci 1965, 1967; Tollestrup 1982; Uptain 1992; Germano and Williams 2005). In extremely dry periods, however, adults may not come above ground for > 21mo (Germano et al. 1994). Females usually produce 3-4 eggs (six maximum) and can produce as many as four clutches by mid-July (Germano and Williams 1992b). Young hatch from July to September and retreat underground beginning in October or early November (Montanucci 1965, 1967; Tollestrup 1979; Germano and Williams 2005).

Montanucci (1965, 1967, 1970) published the first, most comprehensive studies of *G. sila*, but the data are generalized with little quantification. He provides some information comparing valley floor to foothill populations, including differences in size, body pattern, coloration, and scalation. Tollestrup (1982, 1983) also reported on several aspects of *G. sila* population biology; with two of the three study sites on the valley floor and the third was in hills on the west side of the valley, though data were collected for only 2 y. Germano and Williams (2005, 2007) published an extensive data set on 6 y of data on G. sila from a high elevation site on the Elkhorn Plain reporting on body sizes, population abundances, reproduction, sex ratios, growth, survival, and ontogenetic coloration changes of lizards. No other comprehensive studies on demographic characteristics of populations of G. sila have been published since these studies.

To contribute demographic quantification of G. sila, and as part of a larger study (Germano et al. 2012), I collected body size and reproductive data on a population of G. sila in mid-elevation habitat in the southwestern part of their range. The study area was on a bajada (sloping alluvial land) at 122-200 m elevation, above valley floor populations of G. sila that occur between about 30 to 100 m (Montanucci 1965; pers. obs.) and below a site at 740 m elevation in Ephedra scrub habitat (Germano and Williams 2005). I caught and tagged lizards for 10 y throughout the active season of adults extending into August and early September, and I collected data on sex ratios, size structure, activity, and reproduction. I compare these data to populations of this species from valley floor and high elevation habitats. Quantitative ecological data such as these can be useful for determining the conservation needs of this endangered species based on elevational differences of populations, such as life span, growth rates, and reproductive output, which may help focus remediation actions to populations that might be intrinsically more vulnerable to disturbance effects.

MATERIALS AND METHODS

Study site.—The study site was located within the Lokern Natural Area of western Kern County, California, west of the agricultural community of Buttonwillow. The elevation of the site ranged from 122–200 m (Table 1) and was in the central portion of the natural area between state highways 33 and 58 and

TABLE 1. Environmental attributes of study sites of Blunt-nosed Leopard Lizards (*Gambelia sila*) used for elevational comparisons of demographic traits of populations from low to high elevations. The works of Montanucci (1965, 1967, 1970) could not be included because no specific environmental information is given for sites at which he collected data. The elevational range for the Kettleman Hills may not be exact for the study, which did not provide a specific location.

Site	Elevation	Topography	Vegetation	Precipitation	Reference
Pixley	61 m	Flat, valley floor	Annual grasland	about 150 mm annually	Tollestrup 1982
Delano	68 m	Flat, valley floor	Annual grasland	about 150 mm annually	Tollestrup 1982
Kettleman Hills	144–415 m	Rolling hills	Atriplex/annual grassland	about 150 mm annually	Tollestrup 1982
Loken	122–200 m	Bajada	Atriplex scrubland	77–345 mm	This study
Elkhorn Plain	708 m	Bajada	Ephedra scrubland	85–188 mm	Germano and Williams 2005



FIGURE 2. Location of the Lokern study site in the San Joaquin Desert of California, USA (modified from Germano et al. 2012).

Lokern Road (Fig. 2). The study site falls within the boundaries of the San Joaquin Desert (Germano et al. 2011), which has an arid Mediterranean climate with hot, dry summers and cool, wet winters (Dallman 1998). At the town of Buttonwillow, 13.5 km east of the study area, average high temperatures in January are 13.3° C and lows are 2.8° C, and average July daytime highs are 36.1° C and nighttime lows are 19.4° C (http://www.worldclimate.com/climate/us/ california/buttonwillow). Yearly rainfall at the site during the study varied from 77-346 mm (Table 1), although the high was in 1998 at the start of the study was unusually high and the highest yearly total after that was 204 mm (unpubl. data). Precipitation generally occurs November to March with virtually no rain falling from early April through October.

The site was a saltbush scrub (*Atriplex* spp.) desert, with non-native annual grasses and fiddleneck (*Erodium* sp.) covering almost 100% of the ground in wet years (Germano et al. 2012). The site was used to study the effects of livestock grazing on a suite of protected species (Germano et al. 2012). Just as the grazing study was starting in 1997, a wildfire burned more than half of the study site, which eliminated the saltbushes and other smaller shrubs. The rest of the site was prescribed burned two months after the wildfire to make the replicate plots the same by eliminating saltbush (Germano et al. 2012). By 2001 and continuing through 2006, saltbush had reestablished in much, but not all, of the study area (unpubl. data).

Censuses and measurements of lizards.—Over the course of the 10-y study (1997-2006) of cattle grazing on various protected and non-protected species (Germano et al. 2012), I caught G. sila during various phases of the study. Only the relative abundance of G. sila was reported in the grazing study, which was estimated by walking eight (four treatment, four control) 9-ha grids on the study site each year for 10 d, spread out over eight weeks in the spring and early summer. Assistants conducted most of the walking censuses and only recorded lizards they observed, but on some occasions, I also participated in censusing and I caught any G. sila on the plot and recorded size and reproductive information. Also, I caught G. sila when I found them on dirt roads when traveling to and between census plots. From 2002 to 2004, I also conducted a radio-telemetry study of G. sila on the Lokern (Germano and Rathbun 2016), separate from the censuses of lizards for the grazing study. Besides the lizards that I radio collared, I found many additional G. sila while radio tracking and also when traveling between areas where lizards were tagged. Including the trapping that occurred annually for nocturnal rodents and San Joaquin Antelope Squirrels (Ammospermophilus nelsoni) between late July and early September (Germano et al. 2012), I was on the study site and opportunistically catching G. sila from mid-April to early September, the optimal time of adult G. sila activity (Montanucci 1965, 1967; Germano and Williams 2005).

I used a pole and noose to capture lizards. Once a lizard was captured, I noted its location, determined its sex, and applied a numeral to its dorsal surface with a felt-tipped pen. I recorded body measurements using a clear plastic ruler, including snout-vent length (SVL) and total length (TL) to the nearest 1 mm, and recorded mass of each lizard to the nearest 0.1 g using an electronic balance. I also palpated each adult female to determine if she was gravid, and if so, how many eggs she was carrying (Germano and Williams 1992b, 2005). I permanently marked *G. sila* by injecting each lizard (except hatchlings) with a Passive Integrated Transponder (PIT) intra-abdominally (Germano and Williams 1993).

Sex ratios and size comparisons.—The sex of *Gambelia sila* can be determined for all sizes of lizards because males have enlarged post-anal scales (Montanucci 1965; Stebbins 2003). I compared the sex ratio of all individual *G. sila* I caught to 1:1 using Chi-square with Yates correction. I only made statistical comparisons of sizes of male and female

adults (≥ 92 mm SVL) pooling data across years because I was catching lizards almost exclusively before most hatchings were aboveground each year at the study site. I used the smallest size of a female that had eggs (92 mm at this site) as the size at which G. sila became adults on the Lokern (following Germano and Williams 2005). I compared SVL, total length (TL), tail length (TaL; TL-SVL), and mass (g) of males to females using sizes at first capture. I also compared the upper decile SVL, TL, TaL, and mass of adult lizards to minimize the effect of age structure on size estimates (following Case 1976). For TL, TaL, and mass, I did not include any lizards with tails that were not complete or were regrowing after injury, and also for mass, any lizards that appeared emaciated.

Data were normally distributed and homoscedastic, and I used Analysis of Variance (ANOVA) to compare these four measures and their upper decile values of sexes. I also used Analysis of Covariance (ANCOVA) with SVL as the covariate to compare size-adjusted TaL and mass between males and females. Pooling data across years, I compared the distribution of CLs of *G. sila* by month using a Z-test with $Z_{crit} = 2.00$.

Reproduction.—I calculated the percentage of females with eggs by month and compared percentages by month using the Fisher's Exact Test. Because data were not normally distributed even after transformation, I compared the mean number of eggs per female across months using a Kruskal-Wallis Test. I compared the number of eggs in a clutch to SVL using Least-squares Regression. For the regression, I used the largest clutch a female produced during the study if she produced multiple clutches across years.

Elevation comparisons.---I made comparisons of various demographic traits of G. sila from this study to studies by Montanucci (1965, 1967, 1970), Tollestrup (1982), and Germano and Williams (2005), which are the only other studies that reported demographic information. Montanucci did not give specific environmental characteristics of sites for the data he reported, although he did state data were for valley floor and hillside sites. Tollestrup (1982) did specify environmental characteristics and she reported on two valley floor sites and one mid-elevation hillside site (Table 1). The site on the Elkhorn Plain is a high elevational site (Table 1). Other than elevational differences and topography, the sites experience similar temperature regimes (Germano et al. 2011) and precipitation, although the

dominant shrub component (if present) is a species of *Atriplex* on the valley floor and mid-elevations sites but is *Ephedra* scrub at the high elevation site (Table 1). All sites have been invaded by non-native herbaceous plants since the mid-1800s (Germano et al. 2001).

It is difficult to make accurate statistical comparisons of sizes of G. sila at the Lokern site to those at the low elevation valley sites and mid-elevation foothill sites of Montanucci (1965, 1967) and Tollestrup (1982) because the sizes that they report are averages for all adults, not upper decile sizes, which are a better estimate of sizes (Case 1976). Average sizes of all adults are too influenced by reproductive success in prior years such that many small adults skew the average lower than what the actual SVL adults can attain. I did, however, use a One-Sample t-test of average SVL from the field site in this study to point estimates for valley and foothill sites given by Montanucci (1965) to at least give a first approximation of size differences. I could not test data from Tollestrup (1983) because she did not distinguish among sites for sizes.

I made direct comparisons of my size measures to the high-elevation Elkhorn site for upper decile SVL, total length, and mass because analyses were the same as at my mid-elevation Lokern site and the raw data for the Elkhorn site were available to me. Because upper decile SVL for females and upper decile mass for males at both sites were normally distributed and variances between sites were not significantly different, I used ANOVA to compare sites. Male upper decile SVL, total length for both sexes, and non-gravid female mass data were either not normally distributed or were heteroscedastic even after transformation. For these data I compared sites using Mann-Whitney U-tests.

Based on dissected lizards, Tollestrup (1982) reported an average clutch size separately for the valley floor and foothill sites for each of the 2 y she collected egg data. I used a One-Sample t-test on the weighted average clutch size of both years for each site to compare to the mean egg number for the Lokern site. I could not compare my data to that from Montanucci (1965) because he did not distinguish I compared the average number of eggs sites. per clutch from the Lokern site to that of the high elevation Elkhorn site using ANOVA. All means are reported as mean \pm standard error. In all statistical comparisons, $\alpha = 0.05$ and I used the method of Lagendre and Lagendre (1998) to adjust P values for multiple comparisons of size distributions.

				_	Upper 10%	
Trait/Sex	n	Mean	Range	n	Mean	Range
SVL (mm)						
Males	119	107.0 (± 0.57)	92–123	12	117.8 (± 0.71)	115–123
Females	95	103.8 (± 0.66)	92-121	10	114.8 (± 0.87)	112-121
TL (mm)						
Males	111	325.1 (± 1.93)	278–391	11	360.3 (± 3.59)	112–391
Females	87	308.2 (± 2.08)	264–344	9	338.7 (± 1.32)	332–344
TaL (mm)						
Males	111	218.2 (± 1.46)	174–272	11	243.7 (± 3.04)	236–272
Females	87	204.6 (± 1.51)	157–229	9	225.8 (± 0.87)	222–229
Mass (g)						
Males	118	42.26 (± 0.78)	23.7-63.0	10	57.76 (± 0.90)	54.2-63.0
Females	51	33.82 (± 0.93)	22.8-58.1	5	48.80 (± 2.97)	40.3–58.1

TABLE 2. Mean (\pm standard error) and range of values of snout-vent lengths (SVL), total lengths (TL), tail lengths (TaL), and mass of first captures and upper decile (10%) of these traits of the largest individual adult (> 91 mm SVL) Blunt-nosed Leopard Lizards (*Gambelia sila*) captured at the Lokern Natural Area, Kern County, California, USA, 1997–2006. Mass for females is for those without eggs.

RESULTS

I made 361 captures of 119 adult male, 95 adult female, 25 juvenile male, and 25 juvenile female *G. sila* on the Lokern Natural Area. The majority of captures occurred from 2001 to 2006, with only 12 *G. sila* caught from 1997 to 2000. The sex ratio of adult males to females was 1.25:1 but was not significantly different than 1:1 ($X^2 = 2.47$, df = 1, P = 0.116). The average SVL of adult males was 107.0 \pm 0.57 mm and of females was 103.8 \pm 0.66, with the largest male captured 123 mm SVL and the largest female 121 mm SVL (Table 2; Fig. 3). The average SVLs of males and females differed significantly ($F_{1,212} = 13.59$, P < 0.001). The average upper decile SVL of



FIGURE 3. Size distributions of Blunt-nosed Leopard Lizards (*Gambelia sila*) from the Lokern Natural Area, Kern County, California, USA, for first captures of lizards 1997–2006. Males are red bars and females are blue bars.

males was 117.8 ± 0.71 mm and of females was 114.8 mm ± 0.87 (Table 2), and these SVLs also differed significantly between sexes ($F_{1,20} = 6.816$, P = 0.017).

Average TL of males $(325.1 \pm 1.93 \text{ mm})$ and females (308.2 ± 2.08 mm; Table 2) differed significantly($F_{1,212} = 13.59, P < 0.001$), as did average upper decile $TL^{1,18}(F_{1,18} = 24.49, P < 0.001)$. The average TaL of males was 218.2 ± 1.46 mm whereas the average female TaL was 204.6 ± 1.51 mm (Table 2), and these averages also differed significantly $(F_{1.196} = 40.51, P < 0.001)$, as did average upper decile $TaL(F_{1.18} = 24.29, P < 0.001)$. TaL adjusted for SVL, however, was not significantly different between the sexes $(F_{1183} = 0.137, P = 0.712)$. The average mass of non-gravid females was 33.82 ± 0.93 g and that of males was 42.26 ± 0.78 g (Table 2). Average mass and mean upper decile mass differed significantly between males and females (average: $F_{1,167} = 42.55$, P < 0.001; upper decile: $F_{1,18} = 24.49, P < 0.001$) but unlike TaL, mass adjusted for SVL also differed significantly between the sexes ($F_{1,163} = 21.26$, P <0.001) with adult males being heavier than females except at small adult sizes (Fig. 4).

The distribution of sizes of lizards differed among months. The distribution of first captures of individuals in April and May consisted of adults with low numbers of juveniles and small adults, while I only captured adults in June and July (Fig. 5). In August, I caught hatchling and juvenile lizards, although some adults were still aboveground (Fig. 5). By September, I only caught hatchling and juvenile *G. sila* (Fig. 5). The distributions of SVLs in April,



FIGURE 4 Relationship between mass (g) and snout-vent length (mm) of female (dots and solid line) and male (triangles, long dashed line) Blunt-nosed Leopard Lizards (*Gambelia sila*) from the Lokern Natural Area, Kern County, California, USA. The short, dashed lines surrounding the regression lines are the 95% confidence intervals.

May, June, and July differed significantly from the distributions in August and September (Table 3). The distributions of SVLs in April through July did not differ significantly from each other, nor did the distribution of SVLs in August differ from that in September (Table 3).

Over 10 y, females were gravid by late April or early May and still could be found with eggs into very early August. The number of eggs in a clutch, pooling all months, varied from two to five and the average number of eggs from 47 clutches was $3.4 \pm$ 1.09 eggs. The earliest I found females to be gravid was 13 April and 29 April 2004 when both females I caught (SVL = 106 and 104 mm, respectively) were found with three medium-large eggs (Fig. 6). I found females with eggs in all months but September (no adults found), although only one of 11 adult females was gravid in August. This female was small (94 mm SVL) but was carrying three large eggs 2 August 2003. The average number of eggs in a clutch varied by month from 3.0 to 3.6, but these averages across months were not significantly different (H =3.72, df = 3, P = 0.294). The percentage of gravid females that I caught was 50.0% in April, 36.3% in May, 48.9% in June, and 50.0% in July (Fig. 6), but these differences were not significant (Fisher's Exact Test, P = 0.604). The number of eggs in a clutch was significantly related to the SVL of a female ($r^2 =$ 0.387, $F_{136} = 22.74$, P < 0.001), and the relationship is best described as Clutch Size = $0.0686 \times SVL$ -3.681 (Fig. 7).



FIGURE 5. Size distributions by month of Blunt-nosed Leopard Lizards (Gambelia sila) from the Lokern Natural Area, Kern County, California, USA, for first captures of lizards 1997–2006. Males are red bars and females are blue bars.

Comparison	Mean Difference	Ζ	Adjusted P
April-May	6.298	1.65	> 0.05
April-June	8.491	2.24	> 0.05
April-July	6.973	1.79	> 0.05
April-August	12.88	2.70	0.048
April-September	24.29	5.09	< 0.001
May-June	2.192	2.23	> 0.05
May-July	0.675	0.52	> 0.05
May-August	19.18	6.30	< 0.001
May-September	30.58	10.01	< 0.001
June-July	1.517	1.20	> 0.05
June-August	21.37	7.06	< 0.001
June-September	10.80	10.80	< 0.001
July-August	6.309	6.31	< 0.001
July-September	9.905	9.90	< 0.001
August-September	11.41	2.73	> 0.05

TABLE 3. Results of Z-tests comparing distributions of snout-vent lengths by month of Blunt-nosed Leopard Lizards (*Gambelia sila*) captured at the Lokern Natural Area, Kern County, California, USA, 1997–2006. *P* values adjusted for multiple comparisons.

Elevation *comparisons*.—Montanucci (1965)found the average SVL for G. sila from valley sites (92.9 mm, n = 55) to be significantly smaller than for foothill sites (97.8 mm, n = 98). The average SVL for adult G. sila from the Lokern was 105.6 mm (± 0.45 mm, n = 214), which was significantly larger than either the average for the valley floor (t = 28.2, df = 213, P < 0.001), or the foothills (t = 17.4, df = 213, P < 0.001). The upper decile SVLs at the Elkhorn site were 115.8 mm for males and 112.7 mm for females (Germano and Williams 2005). Male upper decile SVLs did not differ significantly between the Lokern and Elkhorn sites (U = 100, P = 0.111), but female upper decile SVLs were significantly smaller at the Elkhorn site ($F_{1,22} = 4.795$, P = 0.039). The upper decile TL of male G. sila at my site was significantly longer than that at the Elkhorn (345.3 mm; U = 140, P < 0.001), as was that for females from the Elkhorn (317.5 mm; U = 139, P < 0.001). For upper decile mass, Lokern males were significantly heavier than Elkhorn males (55.6 g; $F_{1.20} = 51.44$, P < 0.001), but there was no difference in mass of non-gravid females from the Lokern and the Elkhorn (43.4 g; U = 52, P =0.124).

Tollestrup (1982) reported an average of 2.84 eggs/ clutch/year in 1974 and 3.09 in 1975 at the valley floor site, which gave a weighted average of 2.97 across both years. This weighted average was significantly



FIGURE 6. The number of eggs by month in clutches of Bluntnosed Leopard Lizards (*Gambelia sila*) from the Lokern Natural Area, Kern County, California, USA, 1997–2006. The number of females without eggs in May and June is truncated to facilitate pattern comparisons. Actual number of females without eggs in May and June is given at the top of the bars.



FIGURE 7. The relationship between the snout-vent length (mm) of female Blunt-nosed Leopard Lizards (*Gambelia sila*) and the number of eggs produced in a clutch from the Lokern Natural Area, Kern County, California, USA. The solid line is the regression line and the dashed lines are the 95% confidence intervals.

smaller than the 3.4 eggs per clutch I found at the Lokern (t = 4.10, df = 45, P < 0.001). For the foothill site, Tollestrup (1982) reported an average of 3.33 eggs in 1974 and 2.64 eggs in 1975, and the average number of eggs per clutch at the Lokern site also was greater than the weighted average of 2.74 (t = 6.10, df = 45, P < 0.001). The average number of eggs per clutch at the high-elevation Elkhorn site was 3.37 (3.4 in Germano and Williams 2005), which did not differ significantly from the Lokern average of 3.41 ($F_{1.290} = 0.100$, P = 0.762).

DISCUSSION

In some lizard species, elevation has been significantly correlated with changes in growth rate and body size of individuals in populations. For example, female Yarrow's Spiny Lizards (Sceloporus jarrovi) grew more slowly at high versus low elevations (Smith et al. 1994) as did Common Chuckwallas (Sauromalus ater), although chuckwallas were significantly larger at high elevations (Tracy 1999). This was thought to be due to longer availability of food plants at these higher elevations (Tracy 1999). The growth rate of Tasmanian Snow Skinks (Niveoscincus microlepidotus) also was lower at higher elevations (Olsson and Shine 2002), but juvenile Algerian Psammodromus (Psammodromus algirus) grew faster at a high elevation than a low elevation (Iraeta et al. 2006). The average SVL of Eastern Fence Lizards (Sceloporus undulatus) was smaller at higher elevations than lower elevations (Sheridan et al. 2022) but both SVL and mass of Red-bellied Lizards (Sceloporus variabilis) showed a

strong positive relationship with elevation (Ramírez-Bautista et al. 2021). Female body size was not correlated with elevation, however, for the Common Five-lined Skink (*Plestiodon fasciatus*) in the eastern U.S. (Morrissey et al. 2020) or the Mongolia Racerunner (*Eremias argus*) in China (Deme et al. 2022).

Based on average size of all adults and the average upper deciles size, I found that male G. sila were significantly larger than females at this mid-elevation bajada site, although the size of the largest male was 123 mm SVL and the largest female was 121 mm SVL. Montanucci (1965) reported that adult G. sila can be up to 123 mm SVL, but he did not state which sex attained this size or whether this was for the valley floor or hillside sites. The average size of adult G. sila at my site was significantly larger than what Montanucci (1965) reported for either his valley floor or hillside sites, but he likely included hatchlings and juveniles in his size estimates. I was not in the field often enough when offspring hatched to be able to make an accurate estimate of overall average size of G. sila in this population. Tollestrup (1982) reported the average male SVL as 106.1 mm and for females 97.5 mm, and males (up to 120 mm SVL) were significantly larger than females (up to 111 mm SVL). She did not, however, distinguish the two valley sites from her one foothill site other than to state that the sites did not differ. At the high-elevation Elkhorn site, males were significantly larger than females based on upper decile size, although the largest male found in the 6-y study was 118 mm SVL, and two females were almost as large at 116 mm SVL (Germano and Williams 2005). In comparison to the Elkhorn site, adult G. sila at the Lokern were generally longer and heavier. I also found the sex ratio to be 1:1, which is what was found at the Elkhorn site (Germano and Williams 2005). Montanucci (1965) indicated that sex ratios were even on the valley floor but that there were twice as many males as females in foothill habitats; however, he did not show data to support this statement.

Monthly activity patterns are similar among valley floor, mid-elevation, and high-elevation habitats. I found that adult and yearling *G. sila* from the previous year began activity in the following April and a few adults continued activity into the end of August. This is what was found at the high-elevation site (Germano and Williams 2005), but a greater percentage of adults seem to be active into August and even in September on valley floor sites (Montanucci 1965, 1967; Tollestrup 1982; Uptain et al. 1992). At the Lokern and high-elevation sites, G. sila > 100 mmSVL predominated the adult distribution by June and July, although hatchlings and small juveniles were abundant in most years in July at the high-elevation site (Germano and Williams 2005). Although not distinguishing valley floor and hillside sites, both Montanucci (1965) and Tollestrup (1982) show smaller adults (some < 90 mm SVL) in their size distributions of lizards for June and July.

Elevation has also been found to affect reproductive traits in some lizards. In Spain, incubation times of *Psammodromus algirus* differed between elevations (Iraeta et al. 2006). Clutch size decreased with elevation and precipitation in *Plestiodon fasciatus* (Morrissey et al. 2020) but increased with elevation and precipitation in *Sceloporus variabilis* (Ramírez-Bautista et al. 2021). Although clutch mass was not explained by a change in elevation for six populations of *Eremias argus* in China, high-elevation females tended to produce smaller clutches of larger eggs than at lower elevations (Deme et al. 2022).

I found an average clutch size of 3.4 for G. sila at the Lokern, which did not differ significantly from the high-elevation site but was significantly greater than either the valley floor or hillside sites reported by Tollestrup (1982). Montanucci (1970) reported an average clutch size of 3.3 eggs but did not distinguish valley floor from foothill sites. The range of eggs per clutch was similar among sites, with 1-6 eggs from the high-elevation site, 2-5 from my mid-elevation site, 2-5 (Tollestrup 1982) and 2-6 (Montanucci 1970) eggs per clutch for valley floor/hillside sites. Females at my Lokern site were found with eggs starting in April, which also occurred at the highelevation site (Germano and Williams 2005). I found a female with eggs as late as 2 August, but Tollestrup (1982) reported a female with eggs as late 18 August. In contrast, Montanucci (1967) stated that females were gravid only as late as 17 July and the latest gravid females were found in the 6 y of study at the high-elevation Elkhorn site was 22 July. Because there does not seem to be a pattern of differences in average clutch size and last dates females carry eggs based on elevation among these studies, year to year differences in rainfall that could affect arthropod production may be the most important factor in reproductive output.

Finally, there were substantial differences in the percentage of females gravid across months from the Lokern site and the Elkhorn site. As with my study, on the Elkhorn Plain, palpation was used to determine the number of eggs a female was carrying. At the Elkhorn site (combining percentage gravid across years), 32.3% of females were gravid in April, 82.0% in May, 72.9% in June, and 19.8% in July (Germano and Williams 2005). In contrast, I never found > 50.0% of females gravid in any month, although I did find 50% of females (six of 12) gravid in July. The overall high percentage of gravid females in May and June at the Elkhorn site may have been due to exceptionally high grasshopper production in years 3-5 due to substantially increased rainfall after the first two drought years (Germano and Williams 2005). Numbers of grasshoppers at the Lokern site were generally low during the 10-y study, although numbers increased in the last two years (Germano et al. 2012), but these numbers were never close to the extremely large numbers of grasshoppers that occurred on the Elkhorn site.

In summary, there do not seem to be large differences in the population biology of G. sila between valley floor, mid-elevation, and high-elevation habitats. Except for the comparisons between my Lokern site and the high-elevation Elkhorn site, however, comparisons of size, reproduction, and activity to lizards from valley floor populations are limited because of the incomplete nature of studies on the valley floor done in the 1960s and 1970s. Across all sites, adult G. sila are less active by the end of July, but a greater number may remain aboveground on the valley floor into August and September than in mid- and high-elevation populations. Adult lizards at my mid-elevation site generally had larger body sizes and mass than the high-elevation site, and body size was also larger than valley floor sites, but this comparison is equivocal. The most comparable data are the number of eggs per clutch, which were not significantly different between my mid-elevation and the high elevation site but was significantly larger at my site than at the valley floor site. Ultimately, the only way to make accurate comparisons of population characteristics for this endangered species across elevations is to undertake multiple years of study on several valley floor populations collecting the type of data found in this study and the high-elevation study. Also, studying a population of G. sila at a higher elevation than the bajada habitat surrounding the San Joaquin Valley could be useful. Gambelia sila occur in the Panoche Valley in the northern part of the range of the species at elevations of 350-400 m or more, and a comprehensive population study there could greatly illuminate the effect of elevation on this endangered species.

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