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Population Ecology of Blunt-Nosed Leopard Lizards in High Elevation Foothill Habitat

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Abstract.—**We captured 1078 Blunt-Nosed Leopard Lizards (*Gambelia sila*) 2396 times between 1989 and 1994 on the Elkhorn Plain, San Luis Obispo County, California. Based on size at first capture, we caught 119 adult ($\geq$90 mm snout–vent length [SVL]) and 430 hatchling/juvenile ($<$90 mm SVL) males, and 139 adult and 390 hatchling/juvenile females. Sex ratio of males to females was 1.04 (549 males/529 females). Adult *G. sila* generally became active in April, and activity remained relatively high into July. Hatchlings were first noted in either July or August and generally could be found until early November, except in 1990 when no hatchlings were found at any time. Mean number of adults and hatchlings found active each day differed significantly across years, but as many as 32 adults and 42 hatchlings were seen on a plot during a census. Estimates of population abundance on a plot also varied yearly from 20–164 adults and 0–273 hatchling/juveniles and seemed to be affected either by too little or too much rain. Differences in daily activity varied and were moderately well explained by environmental factors. We estimated survivorship of lizards and found 29.0% of hatchlings from 1992 survived to 1993, and 14.6% of hatchlings from 1993 survived to 1994. The oldest *G. sila* found was a female estimated to be 4 years, 10 months when last caught, although most adults were not seen after 2 yr. Growth of individuals varied by year: highest growth rates were for lizards that hatched in 1991 and 1992, and lowest growth occurred in lizards that hatched in 1989. We found adult leopard lizards with eggs in all years but 1990. Females generally were gravid by late April or early May, and some females were found with eggs in early July. Female size at first reproduction was about 90 mm SVL, clutch size ranged from 1–6 eggs, and overall mean clutch size regardless of year or clutch order was 3.4 eggs. Many females produced multiple clutches in a year, and we found up to four clutches by a single female.**

The Blunt-Nosed Leopard Lizard (*Gambelia sila*) once occurred throughout much of the San Joaquin Valley and the adjacent Carrizo Plain and Cuyama Valley in California (Montanucci, 1965; Germano and Williams, 1992a; McGuire, 1996). Much of its range has been lost to agriculture, oil development, and urbanization, and it occurs on less than 15% of its original range (U.S. Fish and Wildlife Service, 1985; Germano and Williams, 1992a; Jennings, 1995). Because of this, *G. sila* has been on the federal list of endangered species since 1967. In the remaining habitat that exists, *G. sila* occurs in desert habitats of alkali sink scrub, saltbush (*Atriplex* sp.) scrub, and grasslands on the valley floor and in saltbush scrub, *Ephedra* scrub, and nonnative grasslands in surrounding foothill areas (Montanucci, 1965; Stebbins, 2003).

The lizard fauna of the San Joaquin Valley is depapaurate with only the Blunt-Nosed Leopard Lizard, Side-Blotched Lizard (*Uta stansburiana*), Western Whiptail (*Aspidoscelis tigris*), and Coast Horned Lizard (*Phrynosoma coronatum*) composing the majority of the species in this area (Montanucci, 1965; Stebbins, 2003; pers. obs.). *Gambelia sila* is the largest lizard of this assemblage and tends to dominate the lizard fauna because it can be abundant and it eats smaller lizards in its habitat, including young of its own species (Montanucci, 1965, 1967; Germano and Williams, 1994). Males are territorial (Montanucci, 1965; Tollestrup, 1983) and they often are conspicuous on rises in the terrain, such as kangaroo rat (*Dipodomys* sp.) mounds, or berms of dirt roads as they survey surrounding territory (pers. obs.). Despite the lizard's large size, relative conspicuousness, and dominant position in the lizard assemblage of the San Joaquin Valley, few ecological studies of the species have been conducted.

The most comprehensive, and earliest, studies of *G. sila* were by Montanucci (1965, 1967). He reported on all aspects of the species' ecology, distribution, and behavior, but the data were generalized with little quantification. Montanucci (1965) proposed that there were identifiable differences in size, sex ratios, and morphology between populations of *G. sila* in the valley and in foothills. Most of his data, however, were from sites on the valley floor. Similarly, Tollestrup (1982, 1983) studied the behavior, ecology, and

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reproduction of *G. sila* at several sites in the San Joaquin Valley, including gathering some reproductive data in the Kettleman Hills on the west side of the valley, but the majority of her data were from two sites on the valley floor. Other works on this species include taxonomic studies, surveys, and short-duration studies and have been summarized in Germano and Williams (1992a) and Jennings (1995).

We studied a population of *G. sila* in foothill habitat in the southwestern part of their range. The study area was at about 708 m (2200 feet) elevation, nearly the highest elevation in the range of the species. We caught and tagged lizards throughout their active season for six years and collected data on sex ratios, size structure, reproduction, growth, activity, and abundance. We compared these population characteristics to the yearly variation in rainfall and herbaceous plant biomass at the area. These data were also compared to data for the species collected previously in valley floor habitats. Because of the endangered status of *G. sila*, quantitative ecological data are vital to its future conservation.

MATERIALS AND METHODS

Study Site.—The study was conducted on the Elkhorn Plain, San Luis Obispo County, California, in the southwestern end of the range of *G. sila*. The Elkhorn Plain is a high-elevation bench at the base of the Temblor Mountains separated from the larger Carrizo Plain by the San Andreas Fault. The climate of the area is Mediterranean with hot, arid summers and cool, moist winters. High temperatures are the norm in the summer, typically ranging from 30–40°C. In winter, nighttime temperatures sometimes drop below freezing, although daytime highs generally are from 10–21°C. The Elkhorn Plain receives less than 200 mm of precipitation most years, sometimes much less. Most rainstorms come in the winter and spring, and the period from May through September is dry.

The plant community of the sites was a shrub-habitat moderately covered by California ephedra (*Ephedra californica*) and eastwoodia (*Eastwoodia elegans*). Also on site were a few Anderson desert thorn (*Lycium andersoni*) and bladder pod (*Isomeris arborea*). The herbaceous ground cover was dominated by the nonnative annuals red brome (*Bromus rubens* ssp. *madritensis*), Arabian grass (*Schismus arabicus*), and red stem filaree (*Erodium cicutarium*). These annuals responded directly to precipitation: they were absent in very low rainfall years and formed dense cover in average or above-average rainfall years.

Censuses and Measurements of Lizards.—*Gambelia sila* were censused on two 8.1-ha plots (plot 1 and plot 2), located about 1.6 km from each other along a dirt road that ran the length of the Elkhorn Plain. Both plots were situated in a mixture of *Ephedra* shrubland and nonnative grassland with a wash running through part of each plot. In addition, the dirt road bisected a portion of each plot. Both plots gently sloped from east to west. Each plot consisted of 16 census lines approximately 277 m long and spaced 18.2 m apart. Wood stakes were placed every 30 m to delineate lines and to mark distances.

From 1989–1994, we censused lizards each month of the lizard's active season when daytime temperatures became high enough for lizards to become active. Preceding each census, we recorded air temperatures 1 cm above the soil, soil temperatures 1 cm below the surface, cloud cover, and relative wind speed (calm, slight breeze, breezy, windy). We used a pole and noose to capture lizards. Once a lizard was captured, we noted its location, determined its sex, and applied a numeral to its dorsal surface with a felt-tipped pen. Each captured lizard was placed in a cloth bag and held until after the census, when we took body measurements, including snout–vent length (SVL) and total length (TL) and recorded mass of each lizard to the nearest gram. Except for 1989, we also palpated each adult female to determine whether she was gravid, and if so, how many eggs she was carrying. We believed that we were accurate because eggs were distinct masses in the body except when eggs became very large, just before laying. Finally, we injected a Passive Integrated Transponder (PIT) subdermally or interabdominally into each Blunt-Nosed Leopard Lizard (Germano and Williams 1993) except for 1989 when we began tagging after June. After all lizards were processed for a day, each lizard was brought back to its original point of capture and released. In all statistical comparisons $\alpha = 0.05$.

Size Comparisons.—To minimize the effect of age structure on size estimates, we used the upper decile size of adult lizards (following Case, 1976) to estimate the average size of males and females. We compared upper decile SVL, TL, and mass between males and females using the nonparametric two-sample Wilcoxon rank sum test because of low sample sizes. We compared the distributions of SVL of lizards at their first capture for each year across years using the Chi-square test of marginal values, with Bonferroni corrections to P-values following the method by Legendre and Legendre (1998). We grouped lizards into four size categories: hatchlings (40–57 mm SVL); juveniles (58–82 mm SVL); small adults (83–97 mm SVL); and adults ($\geq$ 98 mm SVL).

Activity.—Levels of daily activity were estimated from the total counts of leopard lizards found each census irrespective of individual identification. Because population levels were consistently greater on plot 1 than on plot 2, we determined mean daily activity by month on plot 1 for the adult portion of the population from April through September and for the hatchling/juvenile portion from July through October. We compared mean activity on plot 1 among years using ANOVA and Student-Neuman-Kuells (SNK) multirange test of adults using counts from May through July and for hatchlings/juveniles using counts from August and September. To determine proximate environmental factors that affected daily census counts, we used a stepwise multiple regression comparing number of lizards found each census on plot 1 to various factors recorded for that census: year/month of census, time of start of census, relative wind speed at start of census, percentage cloud cover at start of census, air temperature at start of census, and soil temperature at start of census. All factors were added as numerals except for wind speed, which was recorded only as calm, breezy, or windy and was, therefore, coded. We entered single factors and pairwise interactions. We ran separate regression analyses for adults and hatchlings/juveniles.

Population Abundance and Density Estimates.—We estimated size of the adult and hatchling/juvenile portions of the lizard population using a Monte Carlo simulation method (Minta and Mangel 1989) that estimates the population of unmarked lizards. This method is especially useful for capture-resight data of the kind gathered during lizard censuses. The simulation uses the number of marked and unmarked lizards found during censuses. We followed the recommendations of the authors for calculating the lower and upper stopping levels for the simulation and ran the simulation 10,000 times. The total population estimate for this method is the sum of the estimate of unknown lizards from the simulation and the number of animals marked.

Densities of lizards were calculated using the population estimates and the area sampled. From 1992–1994, we measured the perpendicular distance off the census line at which each lizard flushed or was found. These data were gathered to determine the width of census lines on each plot. The distance away from a line that a lizard is detected can vary yearly depending on the amount of vegetative cover. Determining width of census lines is necessary for determining density of *G. sila* on each plot. We computed the area sampled by determining the distance at which 90% of lizards were sighted from census lines. This distance was doubled to determine width of the census line. Both plots consisted of 16 census lines 270 m long and two end lines 300 m long connecting the census lines. Area (square meters) was determined as

$$A = w[16(l' - w) + 2(l'' + w)],$$

where w is the width of the census line, l' is the length of the census lines, and l'' is the length of the end lines.

Survivorship and Longevity.—We estimated survivorship of *G. sila* in 1993 and 1994 by walking meandering lines at approximately 30-m intervals around plot 1 in addition to walking the plot as usual. We walked the area around the plot and captured all surviving lizards that had been marked on the plot as hatchlings/juveniles in previous years but which had moved outside the plot. The area around the plot was surveyed out to about 200 m 19 times from May through July 1993 and 25 times April through July 1994. Survivorship estimates were made for the number of hatchlings lizards marked each year. Longevity was estimated by determining the longest time marked lizards existed on the plot. In some cases, we estimated the month and year of hatching for lizards marked as adults.

Growth.—Somatic growth of *G. sila* was determined for lizards that hatched in 1989 and 1991–1993. Growth estimates were not made for 1990 and 1994 because no lizards hatched in 1990 and insufficient time passed between hatching and the end of the study in 1994 to analyze growth. In spring and early summer of 1990, only small lizards were found. We assumed that any unmarked lizards on the plot hatched in 1989. We included these in growth analyses. No young hatched in 1990. We included small (<95 mm SVL) lizards caught in spring 1991 in the 1989 cohort. We tried to estimate the week in which a lizard hatched each year. In 1989, we assumed hatching to be the first week in August, although not enough censuses were conducted in July to be certain. For 1991–1993, we conducted enough censuses to estimate the beginning of hatching to within a few days. In these years, we also found multiple hatching times based on the small size of some lizards well after other lizards were becoming much larger. We adjusted the estimated hatch date of these small lizards based on the size of the smallest lizards to appear above ground (43–49 mm SVL).

Growth curves were constructed by fitting age (in weeks) and SVL (in millimeters) data to the Richards' growth model (Richards, 1959). The Richards' growth-model was superior to the best-fitting three-parameter model (e.g., Logistic, Gompertz or von Bertalanffy models). The three-parameter models have fixed growth forms and are special cases of the flexible four-parameter Richard's model. This latter model has a variable point of inflection specified by the shape parameter of the growth curve (M; Richards, 1959; Causton, 1969). The Richards' growth model estimates three other parameters using SVL and age data: A, asympototic size; *K*, the growth constant; and I, the point at which curve inflection begins. To solve for SVL at various ages, the model uses the general formula:

$$\mathrm{SVL} = \mathrm{A}\{1 + [M - 1]e^{[-K(\mathrm{Age}-\mathrm{I})]}\}^{(1/(1-M))}.$$

The Richards' model produces less biased estimates of the growth function if the shape of the growth curve differs from that of a fixed-curve model (Leberg et al., 1989). Following recommendations of Bradley et al. (1984), we used mean upper decile sizes of adults as asymptotic sizes because of high values predicted from growth data with large confidence intervals. The only exceptions were for females in 1992 and all groups for 1993 where the model would only run if the asymptote was determined by the model fit. We also included estimates of hatchling size at week 0 to all curve fits using the smallest size of a hatchling found for males (43 mm SVL) and females (45 mm SVL) and the mean size of all hatchlings (48 mm SVL) $<$ 50 mm SVL. We only used lizards with multiple captures because we could estimate their age fairly accurately. In a few instances, SVL of a lizard was recorded as smaller than its previous measurement. Because the bodies of leopard lizards are hard to straighten out to record SVL, we believed these values were underestimates. For individuals in which non-increasing variability existed over multiple measurements, we adjusted measured SVL based on the largest previous measurement. Smaller measurements were increased to the larger previous measurement until a larger SVL was recorded (i.e., to remove decreases in SVL).

Reproduction.—We noted when males and females were within 0.5 m during surveys, which we interpreted as mating behavior, as well as when copulation occurred. Number of eggs was determined by palpation, and multiple clutches in a season were determined by successive recaptures when either the female did not have eggs between clutches or there was a change in number or decreased size of eggs (Germano and Williams, 1992b). We estimated the percentage of females with eggs by month for each year. We compared the mean number of eggs per female across years using ANOVA and SNK multirange test and number of eggs in a clutch to SVL using least-squares regression. We used the largest clutch a female produced in a year if she produced multiple clutches. By combining estimated number of females on each plot with mean size and number of clutches, we determined the minimum number of eggs produced (reproductive output) on each plot each year.

Precipitation and Plant Productivity Measures.—We placed two plastic rain gauges in the study area in 1990 to record precipitation. We used rainfall data collected at a site on the Carrizo Plain (Washburn Ranch), about 12 km west of the Elkhorn Plain, for time preceding when we put out rain gauges. We found that data from the Washburn Ranch gave similar amounts to what was recorded in our gauges.

Annual plant biomass was collected from 120 0.25-m^2 plots from 1991–1994, at the end of the plant growing season. Sixty plots were located near one lizard census plot and 60 near the other census plot, and of these 60, 30 were located on, and 30 off, giant kangaroo rat (*Dipodomys ingens*) burrow systems (a keystone mammal in this area). At each plot, herbaceous plant material was clipped at ground level and placed in a numbered paper bag. Samples were placed in a drying oven. When samples had dried to a uniform weight, they were weighed to the nearest 0.1 g. No sampling was done in 1989 because herbaceous productivity was deemed too sparse to be collected with any precision. An estimate of productivity was made from photographs based on our knowledge of productivity in this area. Productivity was also low in 1990, but we decided to sample it based on 15 0.25-m^2 plots located near one lizard census plot. Samples were statistically analyzed by the Approximate Test of Equality of Means (Sokal and Rohlf, 1981) because of heterogeneous variances among means.

Mulch (plant litter) was gathered in August of each year from 60 0.25-m^2 randomly placed plots near each lizard census plot and placed in a numbered bag. Each sample was cleaned in a bucket of water to remove soil, rocks, and inorganic material. Samples were oven dried until weights were stable and then weighed to the nearest 0.1 g. The mean weight of samples were compared between the plots using a two-tailed *t*-test.

Prey Abundance.—During lizard censuses, we counted numbers of grasshoppers and Side-Blotched Lizards found along census lines. The diet of *G. sila* includes arthropods and small lizards, and grasshoppers, especially, often constitute a large portion of the diet (Meek, 1905; Montanucci 1965, Tollestrup 1979, T. T. Kato, B. R. Rose, and T. P. O'Farrell, unpubl. report). We used counts from plot 1 as an estimate of food abundance. Comparisons of indices of food abundance were made separately for grasshoppers and Side-Blotched Lizards and for separate sets of months corresponding to activity of adults (April through July) and hatchlings/juveniles (July through October). We analyzed these groupings for differences among years using ANOVA and SNK.

RESULTS

Size and Population Characteristics.—We made 2396 captures of 1078 *G. sila* from 1989 to 1994. We captured 549 males, of which 119 were first captured as adults ($\geq$90 mm SVL) and 430 were first caught as hatchlings (44–50 mm SVL) or juveniles, and 529 females, of which 139 were first caught as adults and 390 were first caught as hatchlings or juveniles. Sex ratio of males to females was 1.04, which was not significantly different than 1 to 1 ($\chi^2 = 0.335$, $P = 0.563$). The upper decile SVL of males was 115.8 mm (SE = 0.312, $N = 12$) with the largest male 118 mm SVL. The upper decile SVL of females was 112.7 mm (SE = 0.504, $N = 14$) with the largest female 116 mm SVL. The upper decile of total length of males was 345.3 mm (SE = 1.721, $N = 12$) with the longest male TL 357 mm, whereas for females upper decile TL was 317.5 mm (SE = 1.702, $N = 14$) and greatest TL was 334 mm. Males were also larger by mass: upper decile mass of males was 55.6 g (SE = 0.776, $N = 12$) and greatest mass 60 g, whereas upper decile mass of nongravid females was 42.0 g (SE = 0.660, $N = 14$) with the heaviest nongravid female 47 g. Upper decile mass of gravid females was almost the same as that of males: 53.6 g (SE = 1.078, $N = 14$), and the heaviest gravid females were 62 g ($N = 2$). Males were significantly larger than females on all three measures of size (W = 229–246, all $P < 0.001$).

The smallest lizard caught was a male 43 mm SVL and 2.2 g. Thirty-two *G. sila* were first caught under 50 mm SVL. The mass of lizards under 50 mm SVL ranged from 2.2–4.6 g. Mass was exponentially related to SVL for all individuals and the equation that best described this relationship was mass = $6 \times 10^{-6}\ \mathrm{SVL}^{3.379}$ ($R^2 = 0.971$, $N = 1067$).

Population structure of SVL differed among years. Generally, the distribution of first captures of individuals for each year consisted of adults and hatchlings with low numbers of juveniles and small adults (Fig. 1). However, no hatchling or adult lizards were found in 1990, and this year was excluded from comparisons among years. Even with 1990 excluded, the distribution of SVL of remaining years differed significantly ($\chi^2_{[0.05,\ 12]} = 138.90$, $P < 0.001$). All years differed significantly from each other ($\chi^2_{[0.05,3]} = 68.23$–$9.79$, $P < 0.001$–0.040) except 1989 and 1991 ($\chi^2_{[0.05,3]} = 3.99$, $P = 0.263$). In all years but 1990, the mean SVL of lizards increased from April to June as adult lizards grew, and then increased again from July through October as hatchlings were caught (Fig. 2).

Activity.—Adult *G. sila* generally became active in April and activity remained relatively high into July (Fig. 3). The earliest date when leopard lizards were found was 3 April 1992. Cool, stormy weather often delayed emergence of lizards and earliest dates of first activity in other years varied from 11 April 1994 to 29 April 1991. Adult activity dropped dramatically in August when only a few individuals were found during censuses, and only in 1991 were any adults active in September (Fig. 3). In 1990, only juvenile lizards that had hatched in 1989 came above ground; no adults active in 1989 were found in 1990 nor were larger (> 95 mm SVL) unmarked lizards found. These large juveniles/small adult lizards in 1990 were only active from April until mid-June. Mean numbers of adult *G. sila* seen on plot 1 per day during May through July censuses changed from year to year and differences were significant ($F_{[0.05,5,153]} = 44.65$, $P < 0.001$). Mean numbers varied insignificantly from 2.0–5.4 lizards/census for 1989–1992 ($q = 0.239$–3.614, all $P > 0.05$), but high numbers in 1993 (mean = 17.2) and 1994 (mean = 12.1) were significantly greater than all other years ($q = 7.15$–16.53, all $P < 0.05$) and were significantly different from each other ($q = 6.51$, $P < 0.05$).

Hatchlings were first noted on plots in either July or August 1991–1994 (Fig. 3). Not enough surveys were conducted in 1989 to detect date of first appearance (hatchlings were not seen during 7–10 July but were abundant when plots were next surveyed starting 8 August). No hatchlings were found anytime in 1990. Hatchlings were first found in 1991 on 3 August (last previous survey 24 July), in 1992 on 3 July (last previous survey 2 July), in 1993 on 14 July (last previous survey 12 July), and in 1994 on 15 July (last previous survey 13 July). Juveniles were last found on plots in either late October or early November from 1991–1994 (no late surveys were done in 1989). In 1991, the last juvenile was seen on 8 November, in 1992 on 6 November, 1993 on 8 November, and 1994 on 15 October.

Mean number of hatchlings/juveniles seen per day (Fig. 3) differed significantly from year to year ($F_{[4,100]} = 67.80$, $P < 0.001$) for years when hatchlings were found. Mean numbers of hatchlings/juveniles seen per day were not significantly different in 1989, 1991, and 1994 at 5.0–6.4 sightings ($q = 0.232$–1.19, all $P > 0.05$) but were significantly lower than means of 24.2 in 1992 and 26.5 in 1993 ($q = 11.33$–18.22, all $P < 0.05$). Mean numbers did not differ significantly in 1992 and 1993 ($q = 1.65$, $P > 0.05$).

Daily differences in the number of sightings of lizards were only partially explained by the environmental factors that we recorded. For adults, five factors entered into the regression equation giving $R^2 = 16.95$. The equation that

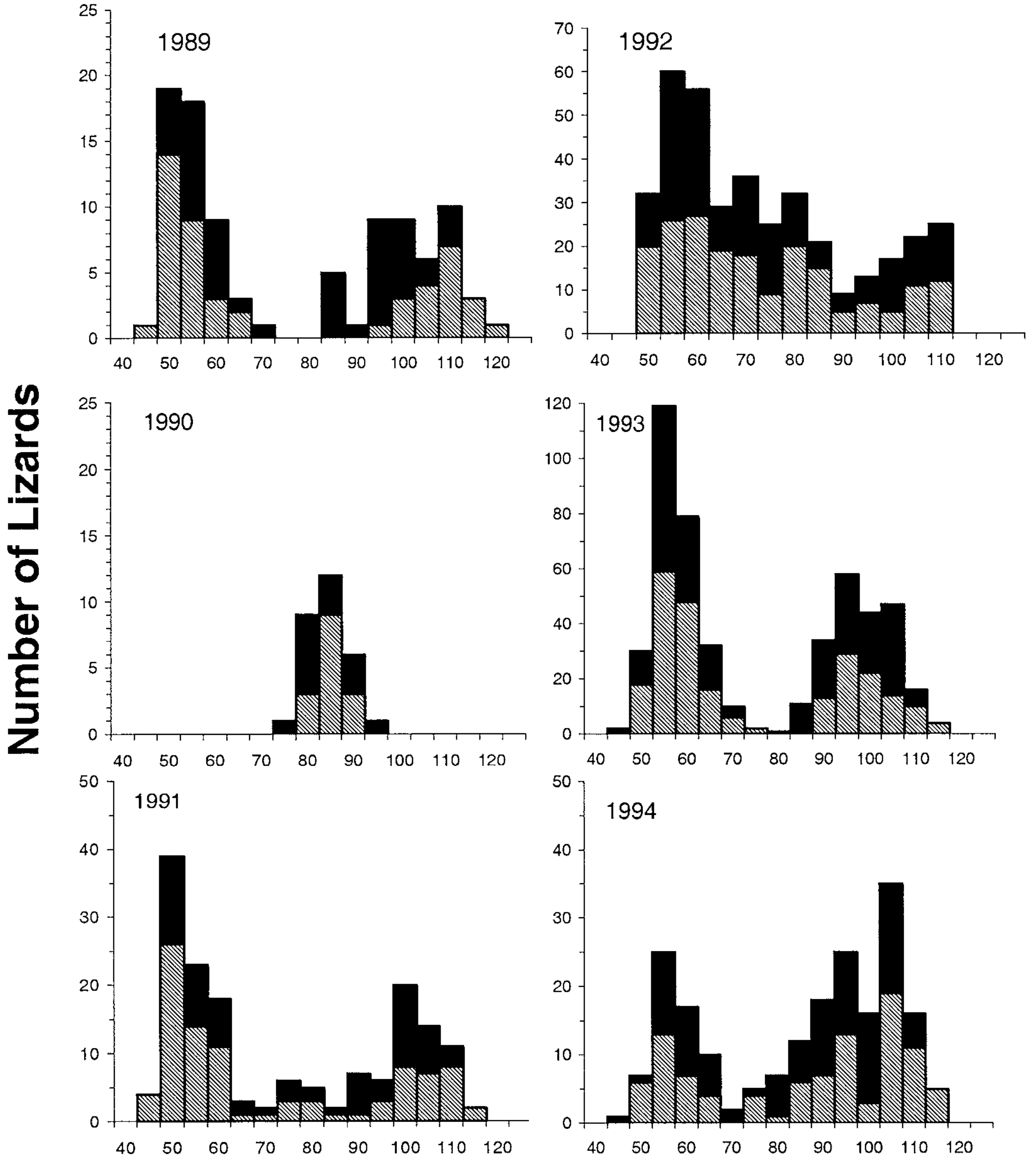

FIG. 1. Size distributions by year of *Gambelia sila* from the Elkhorn Plain, San Luis Obispo County, California, for lizards captured 1989–1994. Males are striped bars, and females are solid bars. Only sizes of lizards at first capture each year were used. Y-axis values vary to facilitate pattern comparisons.

gave the best explanation of the variation in number of lizards seen/day was

$$= 0.00017\,YM \times T - 0.529\,AT + 0.00556\,YM \times CC + 0.207\,ST - 0.0024\,CC \times ST,$$

where *YM* is the year and month of the census, *T* is the time of the start of the census, *AT* is the air temperature, *CC* is the percentage of cloud cover, and *ST* is the soil temperature. Similarly, six factors entered into the model to explain variation in daily numbers of sightings of hatchlings/juveniles. The equation that gave the best explanation had $R^2 = 37.60$ and was

$$= -0.163\,T + 0.288\,YM \times W2 - 5.48\,ST + 0.00435\,T \times ST + 0.84\,AT - 0.32\,YM \times W1,$$

where symbols are the same as for the adult regression, and *W1* and *W2* refer to wind conditions.

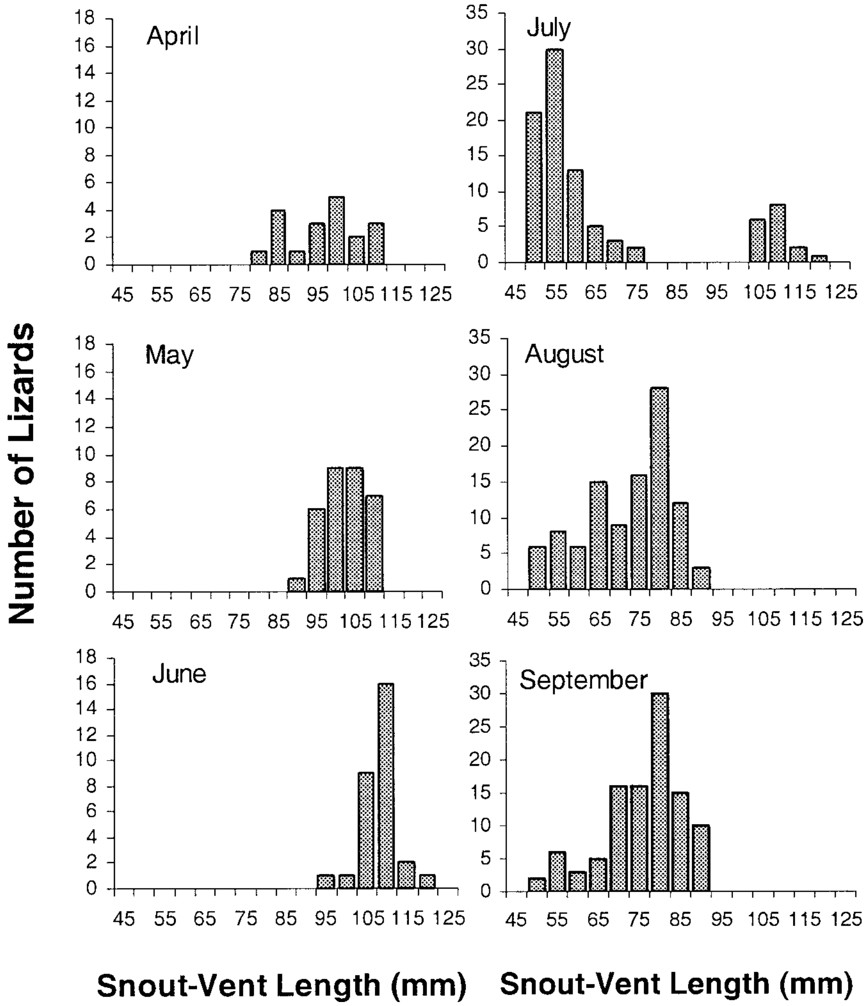

FIG. 2. Size distributions by month of *Gambelia sila* from the Elkhorn Plain, San Luis Obispo County, California, for lizards captured in 1992. Y-axis values vary to facilitate pattern comparisons.

Population Abundance and Density Estimates.—The size of the adult portion of populations of *G. sila* on each plot decreased from 1989 to 1990, increased from 1991 to 1993, and decreased again in 1994 (Table 1). Lizards found in 1990 were probably small adults hatched the previous year. The population estimate of 164 adult lizards in 1993 on plot 1 was over eight times the estimate in 1990. Although numbers of adult leopard lizards dropped to 110 adult lizards on plot 1 in 1994, it was still the second highest estimate recorded. The population estimates of hatchling/juvenile *G. sila* on plot 1 were very high in 1992 and 1993, were at a similar low level in 1989, 1991, and 1994 and were zero in 1990 (Table 1). In 1992 on plot 1, only two years after no hatchlings were found, the population was estimated at 219 young lizards, and reached an estimated 273 in 1993. On plot 2, hatchling leopard lizards increased from 1989 to 1992 (except for 1990) and decreased in 1993 and 1994 (Table 1).

Density estimates were affected by varying levels of grass cover on the plots, which varied the effective width of the census lines. These differences in width of census lines led to differences in area surveyed, which was smallest in 1992 (Table 2). Estimated densities of adult *G. sila* for the last three years of the study ranged from a low of 4.35 adults/ha on plot 2 in 1994 to a high of 16.0 adults/ha on plot 1 in 1993 (Table 2). Hatchling/juvenile densities were highest on both plots in 1992 (23.9–35.6 lizards/ha), and decreased in 1993 and 1994 (Table 2). Plot 1 consistently had higher densities of hatchlings and juveniles than plot 2.

Survivorship and Longevity.—In 1993, almost 30% of hatchlings marked in 1992 were

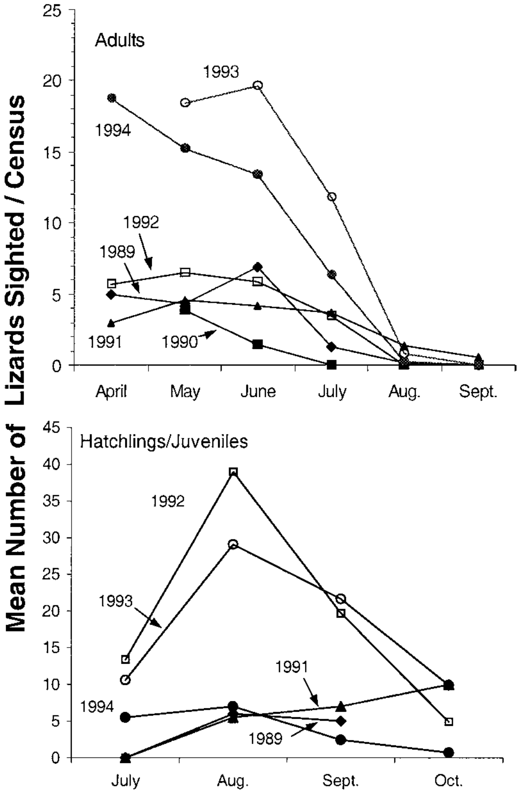

FIG. 3. Mean number of adult (top) and hatchling/juvenile (bottom) *Gambelia sila* active per census by year on plot 1 on the Elkhorn Plain, San Luis Obispo County, California, from 1989–1994. No hatchlings/juveniles were found in 1990.

TABLE 1. Estimated population sizes (95% likelihood intervals in parentheses) of *Gambelia sila* on plot 1 and plot 2 on the Elkhorn Plain, San Luis Obispo County, California, 1989–1994. Months of censuses for adults and yearlings (1st year adults) varied from April to July depending on weather and for hatchlings from July to November. Total marked includes previously marked and newly marked lizards; NCD = the number of census days; significant differences between plots are denoted by asterisks.

Year	Plot	NCD	Total marked	Population estimate
Adults				
1989	1	10	25	40 (33–53)*
	2	10	14	24 (17–36)*
1990	1	22	14[a]	20[a] (17–26)
	2	20	9[a]	19[a] (12–32)
1991	1	22	34	46 (38–68)*
	2	19	21	28 (22–41)*
1992	1	37	54	67 (59–76)*
	2	29	30	45 (38–56)*
1993	1	35	108	164 (149–183)*
	2	34	43	73 (61–87)*
1994	1	39	91	110 (102–123)*
	2	18	40	42 (41–46)*
Hatchlings/Juveniles				
1989	1	12	36	67 (53–88)*
	2	7	13	28 (17–52)*
1990	1	9	0	0
	2	9	0	0
1991	1	30	66	79 (71–90)*
	2	29	41	48 (44–55)*
1992	1	43	186	219 (206–233)*
	2	39	92	107 (99–117)*
1993	1	36	212	273 (251–298)*
	2	34	61	77 (68–89)*
1994	1	41	47	74 (54–90)*
	2	28	17	23 (19–38)*

[a] Numbers represent previous year's hatchlings only; no adults from previous year found.

recaptured, but only about 15% of hatchlings marked in 1993 were found in 1994 (Table 3). Two-year-old lizards had approximately the same survivorship in 1993 as in 1994. No three-year-old lizards were represented in 1993 because no hatchlings were marked in 1990, but 1991 hatchlings, representing three-year-old lizards in 1994, had a minimum survivorship of about 8% (Table 3). No hatchlings marked in 1989 were found in 1993 or 1994.

The oldest *G. sila* lizard found on the Elkhorn Plain was a female estimated to be 4 years, 10 months. She was marked 16 May 1991 at 105 mm SVL and was last found 27 May 1994 at 109 mm SVL. No hatchlings were detected in 1990; hence, we estimated that she must have hatched in August 1989 (when we marked 36 hatchlings). We also estimated six other lizards (two males, four females) to be at least 3 years, 9–11 months. All were estimated to have hatched in August 1989 or, in the case of one male, August 1988.

We documented several factors that led to mortality of *G. sila* on the Elkhorn Plain. We found three adults (two males, one female) on the dirt roads in the plots that appeared to have been killed by vehicles. One small adult female was dead on a plot, but the cause was not known. One adult male standing erect on a kangaroo rat mound was taken by a prairie falcon (*Falco mexicanus*; Germano and Carter, 1995). We also found two instances of adult predation on hatchlings. We saw an adult male catch and swallow a hatchling in August 1991 and an adult female do the same in August 1993 (Germano and Williams, 1994). Although we did not document subsequent mortality, we found a small male in July 1993 with a fleshy projection protruding from its midtorso. Finally, we noted many instances of scars in the outline of adult jaws on the bodies of male lizards. We do not know whether these conspecific attacks led to death, but several glass PIT tags inserted under

TABLE 2. Number of sighting distances (NSD), area sampled (based on perpendicular distances from transect line in m of 90% of sightings), estimated densities (lizards/ha), and 95% confidence intervals (C.I.) for density estimates of *Gambelia sila* on plot 1 and plot 2 on the Elkhorn Plain, San Luis Obispo County, California, 1992–1994. Densities based on estimated population sizes from Table 1.

Year	Plot	NSD	A	Density	95% C.I.
Adults					
1992	1	173	6.81	9.84	8.66–11.2
	2	67	5.21	8.64	7.29–10.7
1993	1	398	10.2	16.0	14.6–17.9
	2	241	10.4	7.02	5.84–8.33
1994	1	294	8.77	12.5	11.6–14.0
	2	98	9.66	4.35	4.24–4.76
Hatchlings/Juveniles					
1992	1	497	6.16	35.6	33.4–37.8
	2	222	4.47	23.9	22.1–26.2
1993	1	700	12.7	21.5	19.8–23.5
	2	274	7.89	9.76	8.62–11.3
1994	1	139	11.5	6.43	4.70–7.83
	2	44	6.48	3.54	2.93–5.86

TABLE 3. Estimated minimum survivorship (%) of *Gambelia sila* on plot 1 on the Elkhorn Plain, San Luis Obispo County, California, 1993–1994. Age group refers to the age class of lizards hatched in a previous year, in parentheses. No hatchlings were found in 1990.

Age group	Number marked	Number found	Survivorship (%)
1993			
1 yr old (1992)	186	54	29.0%
2 yr old (1991)	66	11	16.7%
3 yr old (1990)	—	—	—
4 yr old (1989)	36	0	0%
1994			
1 yr old (1993)	212	31	14.6%
2 yr old (1992)	186	26	14.0%
3 yr old (1991)	66	5	7.6%
4 yr old (1990)	—	—	—
5 yr old (1989)	36	0	0%

the skin were broken in males (Germano and Williams, 1993).

Growth.—Coefficients of determination were relatively high, standard deviations for each parameter were small, and confidence intervals were fairly tight for all growth curves (Table 4), indicating good model fit for all data. Model parameters varied slightly between males and females within years (Table 4). Irrespective of sex, hatchlings grew rapidly in 1991 and 1992, generally reaching 80–90 mm before going underground for the winter (Fig. 4). In contrast, hatchlings grew to about 80 mm SVL in 1993 and only to about 70 mm SVL in 1989 before going underground (Fig. 4). In 1991, several individuals reached maximum SVL in their second year. Significant differences existed among all years in the rate of growth of individuals by week 12 posthatching, with slowest growth occurring in 1989, highest growth in 1991 and 1992, and an intermediate rate of growth in 1993 (Fig. 5).

Reproduction.—We noted mating behavior 35 times in the six years of study: either males and females together ($N = 28$) or copulating ($N = 7$). The earliest we found mating behavior was 22 April (1992) and the latest was 8 July (1993). The majority of mating behavior (82.9%) was seen in May and June. In five instances, males were with females that were gravid, and once a male was seen copulating with a gravid female.

The pattern of reproduction of female *G. sila* varied from year to year. Generally, though, females were gravid by late April or early May and still could be found with eggs into early July (Table 5). In 1989, females were seen to be gravid only in May and June, and no gravid females were found in 1990 when only large juvenile lizards, too small to be reproductive, were active above ground (Fig. 1; Germano et al., 1994). Reproduction was delayed in 1991 when <20% of females were gravid in May, although almost 80% of females were gravid in June. However, only two of 12 females were gravid in July (Table 5). In contrast, in 1992 and 1993, 90–100% of female leopard lizards were gravid in May and June, and >20% were gravid in July. The number of gravid females decreased in 1994 and the greatest percentage of gravid females occurred in May. No females were ever found gravid in August in any year (Table 5). In the four years when we palpated females for eggs, 60–91% of females laid at least one clutch during the year (Table 5).

The earliest a female found to be gravid was 20 April 1994 when two females (SVL = 100 and 101 mm) were found with four eggs each. In 1992, three females (SVL = 98, 98, and 113 mm) were found 27 April with four, four, and six eggs, respectively. In both 1992 and 1994, several surveys of plots occurred in April preceding the dates when females were found with eggs. In 1991, the first gravid female was found 22 May. In 1993, gravid females were found 6 May, but no surveys preceded this date.

The latest dates when a female was still found to be gravid were 22 July 1991 and 22 July 1993. In 1991 a 94-mm SVL female was carrying two eggs and in 1993, a 98-mm SVL female was found with three eggs. In 1992, a 108-mm SVL female was found with three eggs on 14 July. The latest date a female was found with eggs in 1994 was 22 June.

Female size at first reproduction was about 90 mm SVL. The smallest female with eggs was

TABLE 4. Growth parameters (95% confidence intervals) of Richards' growth curves for snout–vent lengths of male and female *Gambelia sila* from the Elkhorn Plain, California, for different years. Parameters describing model fit and growth curves are coefficient of determination (R^2), asymptotic size (A, Upper Decile SVL in millimeters), shape of curve (M), growth constant (K), and inflection point of curve (I).

		Parameter			
	R^2	A	M	K	I
1989					
Males	0.972	115.8	−1.82 (−2.98, −0.66)	0.013 (0.010–0.016)	−86.4 (−131.2, −41.5)
Females	0.942	112.7	0.06 (−1.58, 1.71)	0.016 (0.011–0.020)	−37.5 (−80.6, 5.61)
All Lizards	0.925	114.7	−1.19 (−2.43, 0.06)	0.013 (0.010–0.016)	−75.5 (−119.6, −31.5)
1991					
Males	0.930	115.8	−1.62 (−2.56, −0.67)	0.038 (0.026–0.049)	−27.6 (−42.8, −12.4)
Females	0.943	112.7	−3.00 (−3.59, −2.41)	0.022 (0.017–0.026)	−64.5 (−82.7, −46.3)
All Lizards	0.905	114.7	−3.95 (−4.30, −3.59)	0.015 (0.015–0.016)	−105.1 (−108.4, −101.8)
1992					
Males	0.873	115.8	−3.44 (−3.70, −3.19)	0.016 (0.015–0.017)	−96.5 (−103.6, −89.4)
Females	0.890	103.7[a]	−3.14 (−4.20, −2.07)	0.027 (0.013–0.040)	−53.8 (−88.6, −18.9)
All Lizards	0.866	114.7	−3.73 (−3.93, −3.53)	0.014 (0.013–0.014)	−114.9 (−118.6, −111.2)
1993					
Males	0.910	124.8[a]	−2.93 (−4.41, −1.46)	0.009 (0.007–0.010)	−161.5 (−188.1, −134.8)
Females	0.935	111.0[a]	−3.03 (−3.77, −2.29)	0.013 (0.003–0.023)	−109.5 (−196.2, −22.8)
All Lizards	0.918	120.5[a]	−3.21 (−4.01, −2.42)	0.009 (0.008–0.009)	−169.1 (−186.6, −151.6)

[a] Model estimation.

a lizard 86 mm SVL found 19 May 1993 with four eggs. Also, two females 88 mm SVL and two 89 mm SVL were found gravid. However, the percentage of females < 91 mm SVL with eggs was 30% or less, whereas the percentage of gravid females from 91–94 mm SVL was >60%.

Clutch size ranged from 1–6 eggs (Fig. 6), and overall mean clutch size irrespective of year or clutch order was 3.4 eggs (Table 6). Mean clutch size differed significantly by year from a low of 3.1 eggs/clutch in 1991 to a high of 3.8 eggs/clutch in 1992 ($F_{[3,245]} = 6.34$, $P < 0.001$), and the clutch size in 1992 was significantly greater than all other years ($q = 3.39$–4.49, all $P < 0.05$). We found multiple clutches by females in the four years we palpated females for eggs (Table 6). In 1991 and 1994, we found evidence of at least two clutches in seven females. However, in 1992 and 1993, we found 13 females that produced at least three clutches (four in 1992, nine in 1993) and two females that produced four clutches (one in 1992, one in 1993; Table 6). Mean clutch size by clutch order differed significantly from a low of 3.0 eggs/clutch for second clutches to a high of 3.5 eggs/clutch for the first clutch ($F_{[2,243]} = 5.16$, $P = 0.006$), although clutch size for first clutches was not significantly different than for third clutches (mean = 3.4 eggs; $q = 0.08$, $P < 0.05$). Clutch size increased linearly with increasing SVL of females and was best described by the equation Clutch Size = 0.0672 SVL – 3.19 ($R^2 = 0.234$, $N = 179$; Fig. 6).

On plot 1, reproductive output (number of eggs produced) was estimated to be zero in 1990, 36 in 1991, 138 in 1992, 352 in 1993, and 109 in 1994. On plot 2, reproductive output was estimated as 0, 20, 58, 91, and 32 for 1990–1994. We compared the estimates we made of hatchling numbers to the reproductive output for each plot. The number of hatchlings and juveniles found on a plot was well predicted by reproductive output ($F_{[1,8]} = 34.34$, $P < 0.001$, $R^2 = 0.811$). The equation relating hatchling numbers to reproductive output is: Hatchling Number = 0.774 Reproductive Output + 25.26 ($N = 10$).

Rainfall and Plant/Mulch Productivity.—Rainfall amounts and timing varied considerably on the Elkhorn Plain from 1989–1994. The rain years of 1988–1989 and 1989–1990 were very dry with only 107 and 86 mm recorded, respectively, for the site. Significant amounts of rain did not fall until March 1991, and rainfall amounts were relatively high for the next four years, varying from 158 to 188 mm per year. Herbaceous plant productivity and mulch were closely linked to rainfall, except for 1994, when relatively high rainfall did not produce high levels of plant biomass (Fig. 7). Adult and hatchling abundances also varied with rainfall and plant biomass (Fig. 8). Exceedingly low amounts of rain (and plant biomass) in 1989 and 1990 coincided with low abundances of leopard lizards, whereas increasing rain (and increasing plant biomass) met with increased abundances of lizards until

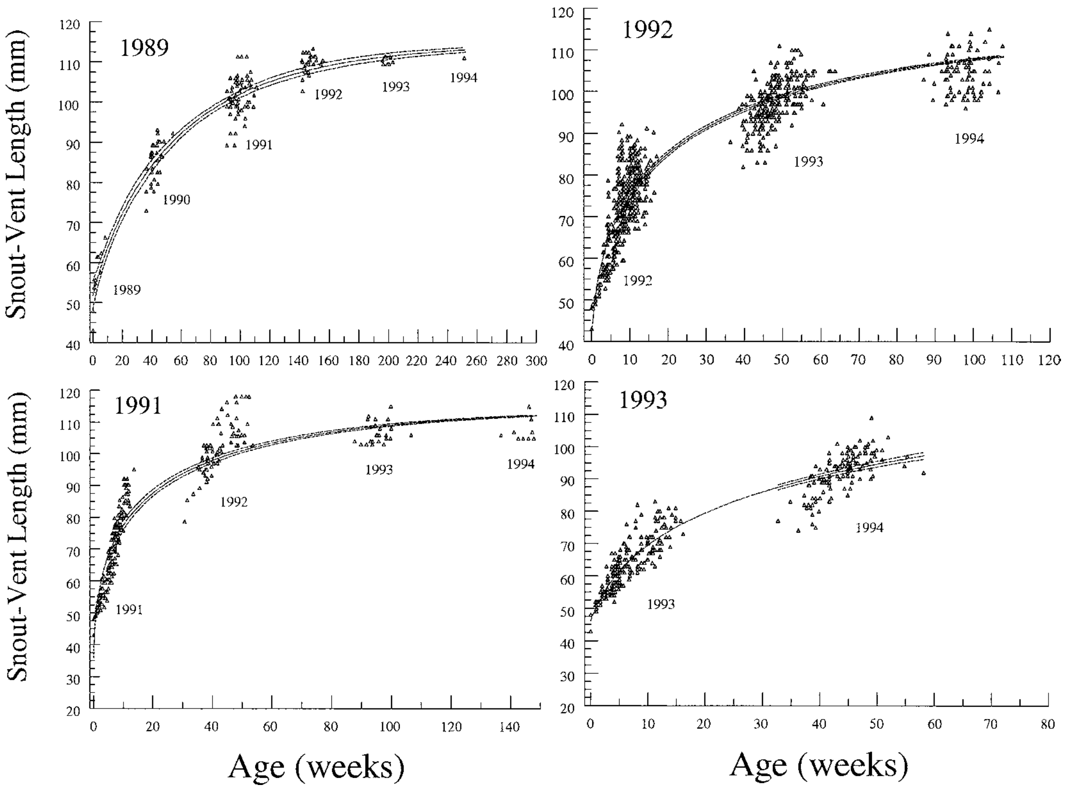

FIG. 4. Growth curves for *Gambelia sila* from the Elkhorn Plain, California, from 1989 and 1991–1993 based on the Richards' growth model. Data for each year are SVL of lizards hatched in that year and measured in subsequent years. Dotted lines are the 95% confidence intervals.

1994, when both adult and hatchling lizard abundances decreased from the previous year. However, correlations of adult and hatchling/juvenile numbers with precipitation were not significant (adult; $r = 0.69$, $P = 0.129$: hatchling/juvenile; $r = 0.66$, $P = 0.157$).

Prey Abundance.—The abundance of grasshoppers and Side-Blotched Lizards also varied from one year to the next on plot 1. The mean number of grasshoppers was extremely low when we first began to count prey in 1990, increased in 1991, was extremely high in 1992, and decreased in 1993 and 1994 (Table 7). Numbers of grasshoppers irrupted in June and July 1992; such high numbers not seen again during the study. Numbers of grasshoppers counted during the period of greatest adult lizard activity (April through July) were significantly different among years ($F_{[0.05,4,144]} = 39.83$, $P < 0.001$), but this was solely because of the high numbers recorded in 1992 ($q = 11.71$–14.87, all $P < 0.05$). Similarly, numbers of grasshoppers counted during the period of greatest hatchling/juvenile lizard activity (July through October) were significantly different among years ($F_{[0.05,4,149]} = 4.45$, $P = 0.002$), again only because of high numbers in 1992 ($q = 3.12$–5.16, all $P < 0.05$).

Although less dramatic, changes also occurred in the mean number of Side-Blotched Lizards found between 1990 and 1994 (Table 7). In the

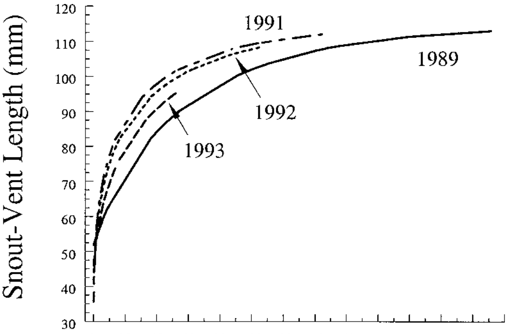

FIG. 5. Comparison of growth curves of *Gambelia sila* from the Elkhorn Plain, California, from 1989 and 1991–1993 based on the Richards' growth model.

TABLE 5. Percentage of female *Gambelia sila* gravid and the mean percentage gravid by month for 1989–1994 on the Elkhorn Plain, San Luis Obispo County, California. Numbers include females caught off the plots. Females with eggs refers to the percentage of adult females ($\geq$ 90 mm SVL) first found in April through June that at some time during the active season produced at least one clutch.

	% Gravid Females						
Month	1989[a]	1990[b]	1991	1992	1993	1994	Mean %
April	—	0	0	27.3	—	38.9	32.3
		(0/1)	(0/1)	(3/11)		(7/18)	(10/31)
May	80.0	—	18.2	100	90.5	74.4	82.0
	(4/5)		(2/11)	(28/28)	(57/63)	(32/43)	(123/150)
June	45.0	—	78.9	90.0	96.7	36.1	72.9
	(9/20)		(15/19)	(18/20)	(58/60)	(13/36)	(113/155)
July	0	—	16.7	23.1	22.8	0	19.8
	(0/3)		(2/12)	(3/13)	(13/57)	(0/6)	(18/91)
August	—	—	0	—	0	0	0
			(0/10)		(0/12)	(0/3)	(0/25)
Females with Eggs	—[c]	0	72.7	91.1	91.1	60.3	80.6
	—	(0/1)	(16/22)	(51/56)	(82/90)	(38/56)	(187/232)

[a] In 1989 only, female leopard lizards were judged gravid by observation, not by palpation.

[b] Only one adult female found: all other leopard lizards < 90 mm SVL.

[c] In 1989, adult leopard lizards were permanently marked after June.

spring and summer (adult *Gambelia* activity), mean numbers of Side-Blotched Lizards were similar in all years except 1992 ($F_{[0.05,4,147]} = 18.36$, $P < 0.001$), which were significantly higher than all other years ($q = 8.42$–9.98, all $P < 0.05$). Mean numbers of Side-Blotched Lizards found during summer and fall (hatchling/juvenile *Gambelia* activity) also differed among years ($F_{[0.05,4,150]} = 22.39$, $P < 0.001$), but these differences were because of high numbers in 1991–1993. The mean of 18.5 in 1991 was significantly larger than all other years ($q = 3.02$–11.7, all $P < 0.05$), and the means in 1992 and 1993 were significantly larger than those in 1990 and 1994 ($q = 4.79$–9.12, all $P < 0.05$). Although adult Side-Blotched Lizards are probably not prey of any but the largest juvenile leopard lizards, hatchling Side-Blotched Lizards can be eaten and usually appeared by late June or early July, becoming relatively abundant soon thereafter. Several times we saw juvenile *G. sila* eating Side-Blotched Lizards almost as large as themselves.

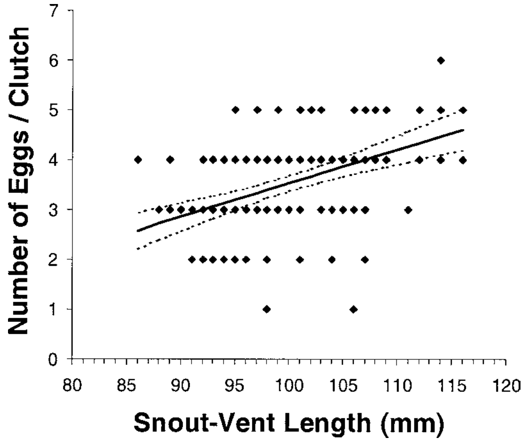

FIG. 6. The relationship between snout–vent length (SVL) and the number of eggs/clutch (95% confidence interval as dotted lines) for female *Gambelia sila* from the Elkhorn Plain, California, from 1991–1994. For females with multiple clutches in a year, only the largest clutch was used.

DISCUSSION

Over the six years of study, the population of *G. sila* on the Elkhorn Plain varied significantly in size and demographic parameters. Numbers of active adult leopard lizards were as low as 20 individuals on an 8.1-ha plot in 1990, when only juveniles that had hatched the previous summer were active above ground, to as many as 164 adults on the plot three years later. The number of hatchlings varied even more dramatically with none found in 1990, and as many as 273 were estimated to be on a plot in 1993. Reproduction and growth also varied over this period. There were significant differences in rainfall during these six years. The area was fairly dry in 1989 and experienced a drought in 1990 but was followed by four relatively wet years starting with an unusually wet March 1991. Herbaceous plant biomass generally followed rainfall with little productivity or mulch in 1989, essentially no production and no mulch on the ground in 1990, and then an increasing level of plant biomass each successive year until 1994 when biomass decreased.

Population stability varies across species groups with birds and mammals about as

TABLE 6. The mean number of eggs per clutch (SE, *N*) by clutch number and by year of *Gambelia sila* on the Elkhorn Plain from 1991 to 1994. No females reproduced in 1990, and no females were palpated for eggs in 1989.

	Number of clutch				
Year	1	2	3	4	Mean clutch size
1991	3.1 (0.31, 16)	2 (0, 1)	—	—	3.1 (0.30, 17)
1992	3.9 (0.16, 41)	3.4 (0.24, 11)	4.0 (0, 4)	3 (0, 1)	3.8 (0.13, 57)
1993	3.4 (0.08, 85)	3.1 (0.12, 33)	3.1 (0.20, 9)	2 (0, 1)	3.3 (0.06, 128)
1994	3.3 (0.12, 38)	2.2 (0.17, 6)	—	—	3.2 (0.12, 44)
Total	3.5 (0.07, 180)	3.0 (0.11, 51)	3.4 (0.18, 13)	2.5 (0.5, 2)	3.4 (0.06, 246)

variable as invertebrates and parasites generally being the most constant (Connell and Sousa, 1983). In contrast, lizards may be almost as stable as parasites (Schoener, 1985). However, examples of lizard populations included few desert species, and those that were included were species much smaller than *G. sila* (Schoener, 1985). Variation in rainfall is generally inversely correlated with amount an area receives: Areas receiving high rainfall have little yearly variation but variation in arid environments is quite high (Trewartha, 1968; Goudie and Wilkerson, 1977; MacMahon and Wagner, 1985). Coupled with temperature, variation in precipitation leads to dramatic changes in plant and insect numbers (Miller and Stebbins, 1964; Beatley, 1969, 1974; Patten 1978; Pitt and Heady, 1978; Hunter et al., 2001). *Gambelia sila* occur in a desert that covers the western and southern portion of the San Joaquin Valley and southwest into the adjacent Carrizo Plain, Elkhorn Plain, and Cuyama Valley (Hawbecker, 1958; Axlerod, 1966; Hafner and Riddle, 1997; Germano et al., 2001). It is not unexpected, therefore, that environmental conditions would vary markedly for this species. In addition, recent invasions of nonnative Mediterranean grasses probably have exacerbated problems faced by this lizard (Germano et al., 2001). In the range of *G. sila*, exotic annual grasses have become the dominant herbaceous component in many habitats (Biswell, 1956; Heady, 1977; Jackson, 1985), particularly the grasses red brome (*Bromus rubens madritensis*), mouse-tail fescue (*Vulpia myuros*), Arabian grass (*Schismus arabicus*), foxtail (*Hordium murinum glaucum*), ripgut brome (*Bromus diandrus*), and soft chess (*Bromus hordeaceus*). These annual grasses respond quickly to increases in rainfall and can cover the ground with dense thickets of stems that leopard lizards likely never encountered before these grass invasions about 150–200 years ago (Germano et al., 2001).

It seems that changes in rainfall and plant biomass directly affected *G. sila*. Certainly, extremely dry conditions seem to have kept adult leopard lizards underground from July 1989 until April 1991. Based on size, only lizards that hatched in 1989 were active in spring 1990, and the period of activity was much shorter than in the other years. We suspect that some adults perished underground, but at least some lizards that were adults in 1989 survived into 1991, despite being relatively inactive for 21 months (Germano et al., 1994; Fig. 1). Although wetter conditions led to increasing numbers of leopard lizards from 1991–1993, their numbers began to decrease in 1994. We do not think this was because plant biomass decreased in 1994. Rather, we suspect that the successive years of increasing plant biomass finally started to negatively affect leopard lizards by the end of 1993. Hatchling survivorship decreased from 1993 to 1994. *Gambelia sila* rely on speed to escape predators and to catch most prey (Montanucci, 1965). A thick cover of herbaceous plants likely impedes the ability of leopard lizards to run. Montanucci (1965) pointed out that dense grass cover negatively affected *G. sila*. Like Montanucci, we actually could catch adult leopard lizards by hand when herbaceous plant cover was high, something we could never do when the ground was more open. If open areas are available, *G. sila* avoid grassy patches. A study of radio-tagged *G. sila* found that lizards were found only on roads and open washes in an area with dense grass growth but were spread out fairly evenly in an area with sparse grass cover (Warrick et al., 1998).

Rainfall and plant biomass also can directly affect the numbers of grasshoppers (Anderson, 1964; Hewitt, 1979; Hunter et al., 2001), a main prey item of *G. sila*. We did find variation in numbers of grasshoppers across years, although these differences were only because of irruptive populations in 1992. Changes in prey number seem to have affected *G. sila* populations. The greatest reproductive output by females was in 1993, the year after grasshopper numbers irrupted. These high numbers of grasshoppers came in

FIG. 7. Photographs of the Elkhorn Plain, California, taken in the spring near the plots used to census *Gambelia sila* showing the amount of herbaceous plant material on the ground when adult lizards were active. Years are 1989 (top left), 1990 (top right), 1991 (middle left), 1992 (middle right), 1993 (bottom left), and 1994 (bottom right).

June and July of 1992 and likely led to females (and males) increasing their stores of fat so that they were in peak physical shape the following spring. The highest percentages of gravid females were found in 1992 and 1993, and females had the greatest number of clutches in these years. Triple and quadruple clutching by females was only seen in 1992 and 1993. High abundance of grasshoppers and *Uta stansburiana* in the summer and fall of 1992 probably also contributed to the higher survivorship of hatchlings into 1993. Greater prey abundance likely also led to high rates of growth of lizards in 1992. Although grasshopper abundance may have affected the demographics of leopard lizards, changes in numbers of grasshoppers did not seem to be directly tied to yearly variation in rainfall or herbaceous plant biomass.

Virtually everything known about the ecology of *G. sila* has come from studies of valley areas. Despite the differences Montanucci (1965, 1967, 1970) found in morphological traits and color patterns between valley and foothill populations of leopard lizards, we found little difference in demographic parameters. 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. We found even sex ratios based on the more than 1000 individuals we caught (hatchlings included). Montanucci (1967) stated that there was no difference in male and female sizes, but Tollestrup (1982) found males (up to 120 mm SVL) to be significantly larger than females (up to 111 mm SVL). We found males to be significantly larger than females based on upper decile size, although the largest male we found in six years of study was 118 mm SVL and two females were almost as large at 116 mm SVL.

Activity patterns are similar among valley floor and foothill habitats. Adult and yearling (previous-year large juveniles) *G. sila* began activity in April on the Elkhorn Plain, and most adult activity ended in July. A few adults continued activity into August and on a few occasions into September. A greater percentage of adults seem to be active into August and September on valley floor sites (Montanucci, 1965, 1967; Tollestrup, 1982; Uptain et al., 1992). Tollestrup (1982) even reported gravid females found into August in one year. We never found a female with eggs past 22 July. No differences were seen between first dates of hatchling appearance in foothill and valley floor sites. We found the first hatchlings from 3 July to early August, which is similar to dates seen on the valley floor (Montanucci, 1967; Tollestrup, 1982). Greatest activity of young-of-year in both areas is in August and September, with activity extending into October on valley floor sites (Montanucci, 1965; Tollestrup, 1982), although we found a few juveniles active into the first week of November in three of the four years we searched this long.

We found the highest abundance and density of *G. sila* recorded in any area. We recorded densities up to 16.0 lizards/ha for adults and 35.6 lizards/ha for hatchlings. Estimates of densities at valley floor sites have only been made for adults and are 0.40 lizards/ha for a site near the Elk Hills (T. T. Kato, B. R. Rose, and T. P. O'Farrell, unpubl. report), 1.1 and 2.6 lizards/ha for two sites in the southern end of the valley (D. L. Chesmore, unpubl. report), 3.3/ha at Pixley National Wildlife Refuge (NWR; Tollestrup, 1979), and 0.3–10.3/ha at eight plots also at Pixley NWR (Uptain et al., 1992). In each case, estimates were made only in one year, and most were based on 10 days of censuses. Even given the limitations of these estimates, valley sites may not support as high a density of *G. sila* as does the Elkhorn Plain. The Elkhorn Plain may represent one of the best remaining habitats of *G. sila*, at least when environmental conditions are favorable (moderate rainfall and sparse grass cover).

Favorable environmental conditions can also lead to fast growth rates of *G. sila*. In 1991 and 1992, several hatchlings grew to $>$ 90 mm SVL before going down for the winter. The largest juvenile found before winter in 1991 was 95 mm SVL and in 1992 was 91 mm SVL. On the valley floor, hatchlings have been found to reach only 85–88 mm SVL before retreating underground (Montanucci, 1967; Tollestrup, 1982). We also found, however, growth is much slower in some years. In 1993, no hatchlings reached 85 mm SVL before becoming inactive; in 1989, when conditions were extremely dry and few grasshoppers were found, most young had not even reached 90 mm SVL by the end of activity in the second year. Conversely, some lizards that had hatched in 1991 reached maximum adult size by their second year. Differences in growth with valley floor sites may only be caused by the wide variation of environmental conditions lizards experienced while we were studying the foothill population.

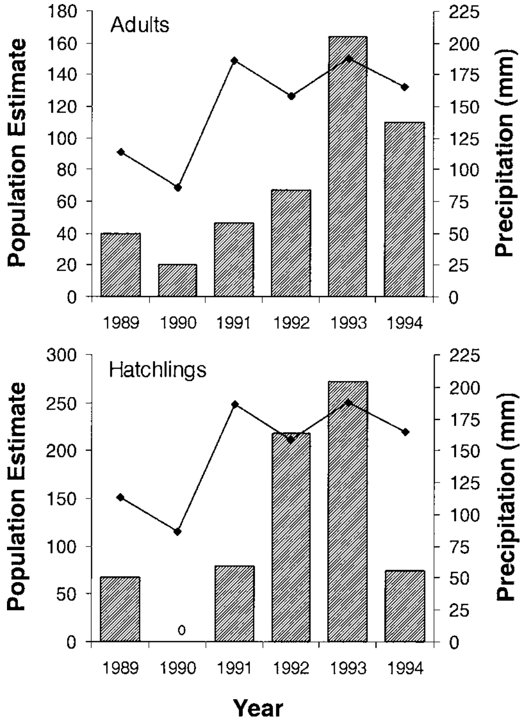

FIG. 8. Relationship between rainfall levels and population estimates of adult (top) and hatchling (bottom) *Gambelia sila* on plot 1 on the Elkhorn Plain, California, from 1989–1994.

Measures of reproduction were somewhat different between foothill and valley floor sites, but this also may simply reflect a greater variation in rainfall during our study. We found that the smallest female reproduced at 86 mm SVL, there was an overall mean clutch size of 3.4 eggs (mean range 3.1–3.8 by year), eggs per clutch ranged from 1–6, and multiple clutching, up to four clutches, was relatively common. In contrast, female lizards on the valley floor also

TABLE 7. Number of surveys (*N*), mean, range, standard error (SE), and 95% confidence interval of grasshoppers and Side-Blotched Lizards (*Uta stansburiana*) counted during censuses of *Gambelia sila* April through July for adults and July through October for hatchlings/juveniles on the Elkhorn Plain, San Luis Obispo County, California, from 1989–1994.

Year	*N*	Mean	Range	SE	Low 95% CL	High 95% CL
Grasshoppers (April through July)						
1990	20	20.5	5–40	2.51	15.2	25.7
1991	18	140.2	3–332	21.58	94.7	185.8
1992	37	5566.7	29–13500	749.59	4046.5	7087.0
1993	35	195.7	3–497	23.28	148.4	243.0
1994	39	61.8	8–238	8.63	44.3	79.3
Uta (April through July)						
1990	21	3.2	1–8	0.47	2.21	4.17
1991	21	3.6	0–8	0.55	2.41	4.73
1992	36	11.3	3–39	1.35	8.51	14.0
1993	35	3.8	0–13	0.57	2.67	4.99
1994	39	3.6	0–10	0.47	2.63	4.55
Grasshoppers (July through October)						
1990	9	12.6	6–21	1.81	8.4	16.7
1991	30	387.9	114–767	40.5	305.0	470.8
1992	37	1090.8	1–9600	432.2	214.3	1967.4
1993	37	21.2	7–76	2.68	15.7	26.6
1994	41	18.3	2–41	1.54	15.2	21.4
Uta (July through October)						
1990	10	5.4	1–13	1.15	2.8	8.0
1991	30	18.5	3–43	1.78	14.9	22.1
1992	37	14.2	1–39	1.67	10.8	17.6
1993	37	14.7	1–31	0.92	12.8	16.5
1994	41	4.0	0–10	0.39	3.2	4.8

can start reproducing by 86 mm SVL, but females produce 2.9–3.3 eggs per clutch, clutch size ranges from 2–5 eggs, and only a few females produce a second clutch (Montanucci, 1965, 1967; Tollestrup, 1982). We suspect that the somewhat smaller clutch sizes and fewer clutches in a year for valley floor populations are because lizards on the Elkhorn Plain experienced two very good years, particularly because of irruptive populations of grasshoppers in 1992 that were not seen during studies at valley floor sites.

Gambelia sila are most closely related to Long-Nosed Leopard Lizards (*G. wislizenii*); in fact, *G. sila* was considered a subspecies of *G. wislizenii* for many decades (Montanucci, 1970; Jennings, 1995; McGuire, 1996). In *G. wislizenii*, females are larger than males, and females can reach up to 143 mm SVL (Parker and Pianka, 1976; Tollestrup, 1982), considerably larger than *G. sila*. A summary of various studies of reproductive traits of leopard lizards by Parker and Pianka (1976) shows that female *G. wislizenii* mature between 89 and 95 mm SVL, similar to *G. sila*, but clutch size is larger (mean 3.4–7.3) and a clutch can be up to 11 eggs. The only density estimates for *G. wislizenii* has been from fenced populations in southern Nevada, and densities ranged from 1.23–3.05 adult lizards/ha for three plots over five years (Turner et al., 1969). These values are similar to what has been seen for *G. sila* on the valley floor but less than what we found for the three high abundance years on the Elkhorn Plain. Finally, we have estimated a minimum longevity of about 58 months for one female *G. sila*, and several adults lived to at least 46 months. In comparison, two male *G. wislizenii* have been estimated to have lived at least to 117 and 118 months (almost 10 yr), and one female lived to at least 82 months (Medica and Turner, 1984). Obviously we only followed lizards for six years, and our plots were not fenced, which may account for the differences in estimates.

There do not seem to be large differences in the ecology of *G. sila* between valley floor and foothill habitats. We did find large variation in numbers, reproduction, and growth rates of leopard lizards on the Elkhorn Plain that seem to be linked, at least partially, to large variation in rainfall, herbaceous plant production, and prey abundance. These large swings in abundance can be detrimental to the conservation of this species, inasmuch as *G. sila* occupy only a small fraction of their former range and some of the remaining range is highly fragmented (Germano and Williams, 1992a; Jennings 1995). It seems that either very dry or moderately wet years depress leopard lizard populations, which could lead to local extinctions in small blocks of habitat. Without source populations of lizards, isolated blocks of habitat may lose this species during adverse environmental times. Exacerbating this problem is the thick cover of nonnative grass that occurs in average to above-average rainfall years. Without some means of diminishing this grass cover in these years (Germano et al., 2001), populations of *G. sila* could be in trouble throughout their range.

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