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David J. Germano

Department of Biology, California State University, Bakersfield, CA 93311, dgermano@csub.edu

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Activity and thermal biology of Blunt-nosed Leopard Lizards (*Gambelia sila*) in the San Joaquin Desert of California

DAVID J. GERMANO^{1,*}

¹Department of Biology, California State University, Bakersfield, CA 93311

ABSTRACT.—Because lizards are ectotherms, their life-history traits are greatly influenced by variations in thermal regimes. The Blunt-nosed Leopard Lizard (*Gambelia sila*) is an endangered lizard that dominates the lizard community in the San Joaquin Desert. Because of the protected status of the species, census protocols are in place to ensure that censuses are conducted during optimal times for lizard activity, but the protocols have not been evaluated by a detailed study. Also, because of changing thermal regimes as a result of climate change, there is concern for lizard species worldwide. I studied the activity and thermal biology of *G. sila* in 2003 and 2004 on the Lokern area of the San Joaquin Desert using data from radio-collared lizards. I also gathered thermal data from cloacal temperatures of *G. sila* in 1991 from the Elkhorn Plain in another part of the desert. From these data, I found that survey protocols do not set optimal times or temperatures to most effectively census this species, and that despite projected rising temperatures, *G. sila* may not become imperiled by a moderate change in thermal regime.

RESUMEN.—Debido a que los lagartos son ectotérmicos las características de su historia de vida son afectadas por las variaciones en los regímenes térmicos. El lagarto *Gambelia sila* es una lagarto en peligro de extinción que domina la comunidad de lagartos en el desierto de San Joaquín. Por su condición de protección, los protocolos de censo empleados garantizan que los estos ocurran durante el horario de mayor actividad de los lagartos. Sin embargo, su eficacia no ha sido confirmada mediante un trabajo detallado. Además, debido a los cambios en los regímenes térmicos como resultado del cambio climático, existe una gran preocupación por las especies de lagartos en todo el mundo. Durante los años 2003 y 2004, estudié la actividad y la biología térmica de los lagartos *G. sila* en el área Lokern del desierto de San Joaquín, utilizando la información obtenida de lagartos con radio collares. También reuní información térmica de los lagartos *G. sila* proveniente de temperaturas cloacales registradas en el año 1991 en la llanura Elkhorn, en otra zona del desierto. A partir de estos datos, encontré que los protocolos de medición no establecen tiempos o temperaturas óptimas para censar más efectivamente a esta especie y que, a pesar de se ha proyectado un aumento de temperatura, no es posible predecir que los lagartos *G. sila* se encuentren amenazados por un cambio moderado en el régimen térmico.

Because lizards are ectotherms, their life-history traits are greatly influenced by variations in environmental conditions. For example, time of activity of diurnal lizards is strongly influenced by temperatures but can also be limited by several factors, including the species, the physical features of the habitat, the predators, the competitors, and the availability of food and water (Huey 1982). Using flexible behavior and physiology, diurnal lizards can maintain a high body temperature when active (Cowles and Bogert 1944, Huey 1982, Bradshaw 1986, Adolph and Porter 1993). Various physiological measures of lizard performance, such as metabolic rate, burst speed, endurance, and digestive efficiency, are affected by both ambient and body temperature (Angilletta et al. 2002, Sears et al. 2016),

and heliothermic lizards have body temperatures that result in the highest performance values of active lizards (Huey 1982).

The Blunt-nosed Leopard Lizard (*Gambelia sila*) is a diurnal heliothermic lizard endemic to the San Joaquin Desert (Germano et al. 2011) and is the largest lizard in a depauperate lizard community (Montanucci 1965, Germano 2009). Adult males are significantly larger than adult females (upper decile SVL = about 116 mm for males and about 113 mm for females), and males are territorial (Montanucci 1965, Tollestrup 1983, Germano and Williams 2005). *Gambelia sila* is an active predator that mainly eats invertebrates, especially coleopterans and orthopterans (Montanucci 1965, Germano et al. 2007). Habitats of *G. sila* range from *Ephedra* scrub at higher elevations to saltbush

*Corresponding author: dgermano@csub.edu

(*Atriplex* spp.) scrub and alkali sink scrub at lower elevations (Montanucci 1965, Germano 2009, Stewart et al. 2019). Exotic herbaceous plants have invaded these areas and have aided the spread of wildfires, creating shrubless grasslands that *G. sila* uses (Montanucci 1965, Germano and Williams 1992, USFWS 1998, Germano 2009). This lizard is also a state- and federally listed endangered species (USFWS 1998). Because *G. sila* is endangered, there is considerable census monitoring. Surveyors are required to follow protocols that include general ecological and physiological data collection; however, detailed information about time of activity and temperature are unavailable from these surveys and are not in the scientific literature. Detailed data such as these are useful for determining the best times and conditions to search for this endangered lizard and could also be important in predicting how populations of *G. sila* might respond to climate change.

METHODS

Study Sites

I collected activity and thermal data on *G. sila* in 2003 and 2004 on the Lokern Natural Area of western Kern County, California (35° 22' 24" N 119° 36' 33" W, datum WGS84), located in the San Joaquin Desert. The Lokern Natural Area encompasses about 17,800 ha (44,000 acres) at an elevation of 122–200 m above sea level (asl). The climate of the area is Mediterranean, with hot, arid summers, cool, moist winters, and rainfall averaging only about 170 mm (Germano et al. 2012). About 8 km northeast of the study site (Buena Vista Water Storage District, Buttonwillow, CA) average high temperatures were 29.6 °C in May 2003, 30.1 °C in May 2004, 34.3 °C in June 2003, 33.6 °C in June 2004, 37.8 °C in July 2003, 36.4 °C in July 2004, 35.1 °C in August 2003, and 35.4 °C in August 2004. The Lokern study site is a gently sloping (2% to 5%) alluvial plain with soils classified as Kimberlina sandy loam and Kimberlina gravelly sandy loam, which are derived mostly from granitic and sedimentary rock (Soil Conservation Service 1988). Wildfire occurred across about half of the study site in 1997, and 2 months later the rest of the site was burned (Germano et al. 2012). By 2000, nonnative grasses dominated portions of the area, while native valley saltbush (*Atriplex polycarpa*) and

spiny saltbush (*A. spinifera*) dominated other portions (Germano et al. 2012). The herbaceous ground cover in both the grass and scrub portions was dominated by the nonnative annual red brome (*Bromus rubens* ssp. *madritensis*), Arabian grass (*Schismus arabicus*), and redstem filaree (*Erodium cicutarium*).

I also collected cloacal temperature data on *G. sila* from the Elkhorn Plain, San Luis Obispo County, California, from May to August 1991. The Elkhorn Plain is also within the San Joaquin Desert, at about 750 m asl southwest of the Lokern study site on the western base of the Temblor Mountains (Germano et al. 2011). It has a climate similar to the Lokern site. Despite spatial and elevational differences between the Lokern site and the Elkhorn Plain, leopard lizards from those areas belong to the same genetic subunit (Grimes et al. 2014, Richmond et al. 2017). The plant community at the Elkhorn site was a grassland and shrub mosaic dominated with scattered California ephedra (*Ephedra californica*) and yellow aster (*Eastwoodia elegans*). Anderson's desert thorn (*Lycium andersonii*) and bladder pod (*Isomeris arborea*) were also on this site in low abundance. As at the Lokern study site, herbaceous ground cover was dominated by red brome, Arabian grass, and redstem filaree.

Activity

From 2002 to 2004, I used radio transmitters (model BD-2G, Holohil Systems Ltd., Carp, Ontario, Canada) attached to lizards via beaded-chain collars (Harker et al. 1999, Germano and Rathbun 2016) to determine home ranges on the Lokern Natural Area (Germano and Rathbun 2016). Additional data collected at the same time provided information on activity times. Project assistants and I located radio-marked lizards on foot or by driving roads. We used digital telemetry receivers (model R-1000, Communications Specialists Inc., Orange, CA) paired with an H-Adcock or 3-element Yagi antenna. Universal Transverse Mercator (UTM) coordinates of all loci were determined with a GPS receiver (Trimble GeoExplorer 3) with differential and real-time correction. From 5 May 2003 to 23 June 2003, I collared 32 *G. sila* (18 males, 14 females), and from 13 April 2004 to 14 June 2004, I collared 33 *G. sila* (18 males, 6 radio-marked in 2003; 15 females,

5 radio-marked in 2003). Lizards were radio-located once a day 3–5 times per week until late July to early August, which is the end of the active season for most adults. I did not collect enough locations of collared lizards in 2002 to make meaningful comparisons to locations from 2003 and 2004, so the 2002 data were not used. Assistants and I tracked lizards during daylight, usually from about 0800 to 1300, when lizards were often aboveground. I also relocated lizards during the late afternoon to determine at what temperatures and times Blunt-nosed Leopard Lizards retreated to burrows for the night.

By tracking lizards, I was able to determine the percentage of radio-locations where lizards were aboveground and belowground across daily times and temperatures. Because lizards are a dark color when cool, I also noted the color of lizards located in the morning, with the assumption that darker lizards had emerged recently from their overnight burrow. I also noted whether lizards were in shade or in full sun and whether they were up in live shrub canopies or on dead branches of burned saltbush.

Thermal Biology

During the radio-tracking on the Lokern site, I recorded the air temperature 1.5 cm above the ground (surface temperature) whenever I radio-located a lizard. In 2004, I also attached temperature-sensitive radio transmitters (model BD-2G, Holohil Systems Ltd.) to 4 male *G. sila*, which I followed throughout most of the active season (May–August). The pulse rate of these radio transmitters consistently varied with the transmitter temperature. I used a graph of this relationship for each transmitter to determine the proxy body temperature (°C) of each lizard, considering that lizards are ectotherms.

On the Elkhorn Plain from May 1991 to August 1991, I used a digital thermometer to record the cloacal temperature of adult leopard lizards at the time of capture. I inserted the tip of the thermometer about 1.5 cm into the cloaca and recorded temperature when it stabilized (usually within 1 min). I then immediately recorded air temperature at chest height (about 1.3 m above the ground) in May 1991. From June 1991 to August 1991, I repeated the procedure, but I recorded the surface temperatures.

Data Analysis

I compared the distributions of the times of emergence (estimated with sightings of dark-colored lizards) for male and female *G. sila* using the Kolmogorov–Smirnov (K–S) test. I compared the mean surface temperatures between males and females when they first emerged from night burrows using analysis of variance (ANOVA). To compare the percentage of lizards in the shade of a live or dead saltbush to the surface temperature, I used Pearson's product moment correlation (PPMC), and to compare the percentage use of this same habitat hourly for males and females between 0700 and 1900 I used the K–S test. I also used the K–S test to compare the percentage distribution of males and females in the shade of bushes with associated surface temperatures at intervals of 2 °C between 20 °C and 48 °C.

Average regional high air temperatures varied by month (Buena Vista Water Storage District at Buttonwillow). I used PPMC to determine whether there were correlations of surface temperature to time of day (up to 1759) by month (May–August). I compared the percentage of locations of lizards that were aboveground at various temperatures (20–22 °C, 22–24 °C, 24–26 °C . . . , up to 46–48 °C) by months (May–August), rounding percentages to integers and testing using a contingency table. I compared temperature distributions of monthly pairs (May–June, May–July, etc.) with a contingency table, adjusting *P*-values for the 6 comparisons by following the method of Legendre and Legendre (1998).

Occasionally lizards were found on plants on the Lokern Natural Area. I compared the time and temperature distributions of males and females when they were up in live saltbush shrubs, on dead branches (sticks) of burned saltbush, or on Russian thistle (*Salsola* spp.). Because the percentage of locations was low for lizards on live saltbush and Russian thistle, I combined numbers on both plants for each sex and compared sexes using Fisher's exact test. The total number of aboveground locations of females (941) was 79% of the number of male locations (1190), so I prorated the number of male locations to match the percentage of aboveground locations of females because goodness-of-fit tests are sensitive to sample size.

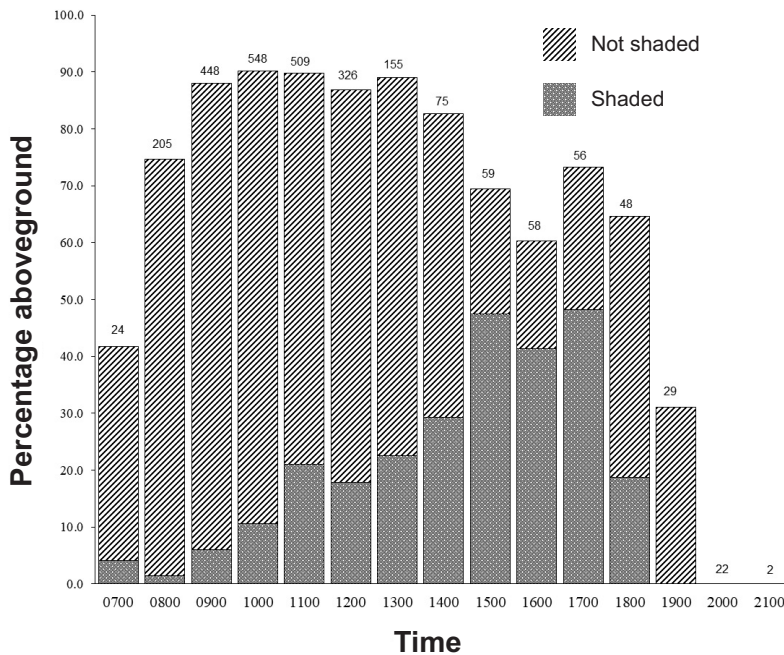


Fig. 1. Percentage of locations of radio-collared Blunt-nosed Leopard Lizards (*Gambelia sila*) found aboveground at differing time periods (0700 = 0700–0759, 0800 = 0800–0859, etc.) from May to August 2003–2004 at the Lokern Natural Area, Kern County, California. Darker shading within bars represents locations of lizards aboveground that were in the shade of either a live saltbush (*Atriplex* spp.) or the dead branches of burned saltbush.

For lizards carrying temperature-sensitive radio transmitters on the Lokern site, I used regression to compare surface temperatures to radio temperatures when the lizards were in burrows, in full sun, and in shade. I also compared mean transmitter temperatures when the lizards were in burrows, in full sun, and in shade using a Kruskal–Wallis test because the data were heteroscedastic even after transformation. For 3 of the males carrying temperature-sensitive transmitters (the collar came off one lizard), I also recorded temperatures of their transmitters when the lizards had retreated into a burrow for the season (based on plugged burrows; see results). I used regression to determine whether there was a relationship between transmitter temperature and air temperature for times when lizards were in plugged burrows. I compared slopes and intercepts of significant regressions for the Lokern data using ANCOVA. For lizards on the Elkhorn Plain, I analyzed the relationships between cloacal temperature and air temperature (about 1.3 m above the ground surface) and between cloacal and surface temperatures using regression. For all statistical tests, $\alpha = 0.05$.

RESULTS

Activity

Of 2148 *G. sila* locations taken from 0700 to 2100, 83.8% were aboveground. I found lizards aboveground as early as 0720 on 5 July 2003 and as late as 1946 on 23 July 2003 (Fig. 1). From 0700 to 0759, 41.7% (10 of 24) were aboveground, but only one was aboveground before 0745. The percentage of aboveground locations rose to 74.6% from 0800 to 0859 and was 80%–90% from 0900 to 1400 (Fig. 1). From 1500 to 1859, the percentage of aboveground locations varied from 60.3% to 73.2%. From 1900 to 1959, the percentage dropped to 31.0% (9 of 29), and none were aboveground after 2000 (Fig. 1). From 0700 to 1800, surface temperature was significantly correlated to time across all months of adult activity (Table 1).

The percentage of locations from 0730 to 1059 when *G. sila* were dark colored varied from 0.4% to 63.8% (Fig. 2). From 0730 to 0859, the percentage of locations when lizards were dark was >40%, but by 0900 to 0929, the percentage dropped to 17.8% (Fig. 2). The

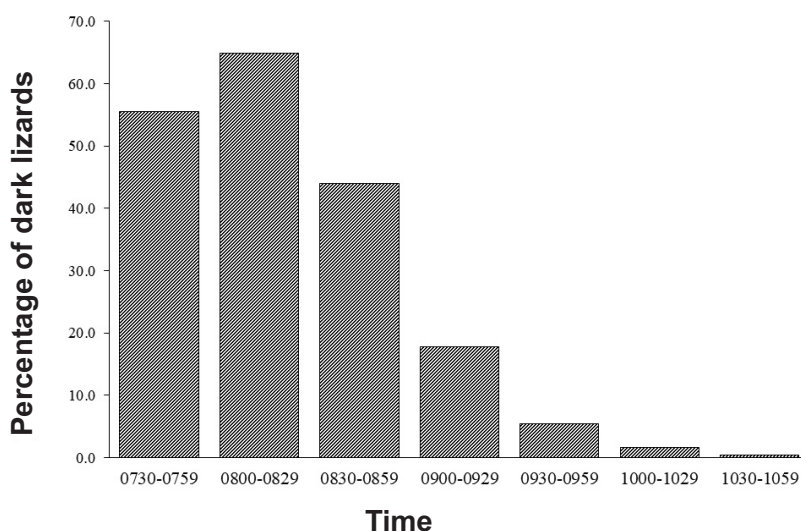


Fig. 2. Percentage of locations by half-hour time periods at which dark-colored Blunt-nosed Leopard Lizards (*Gambelia sila*) were observed, May to August 2003–2004, at the Lokern Natural Area, Kern County, California.

TABLE 1. Correlation coefficient (r), sample size (n), t value, and P value for surface temperature (shaded, 2 cm above the ground) versus time (0700–1800) by month (2003 and 2004 combined) on the Lokern Natural Area, Kern County, California. An asterisk (*) indicates a significant correlation ($\alpha = 0.05$)

Month	r	n	t	P
May	0.332	564	8.34	<0.001*
June	0.532	921	19.0	<0.001*
July	0.663	638	22.3	<0.001*
August	0.561	100	6.20	<0.001*

distribution of the number of locations of dark males across these times did not differ significantly from that of females ($D = 0.100$, $P = 1.000$).

Some lizards were in the shade of live or burned saltbushes across all hourly periods except 1900–2059 (Fig. 1). The highest percentages of lizards in shade were observed from 1500 to 1859 and varied from 65.9% to 68.6% (Fig. 1). The distribution of the percentage of locations of lizards in the sun or in the shade differed significantly across time periods ($D = 0.667$, $P = 0.005$), but not between males and females ($D = 0.154$, $P = 0.995$). I also found that *G. sila* climbed up Russian thistles and living, dead, or burned saltbushes (Fig. 3), but this behavior only accounted for 4.60% (98 of 2131) of locations when lizards were not in burrows. Males differed significantly from females (Fisher's exact test, $P = 0.011$), with

11 males on live saltbushes, 50 on dead saltbushes, and none on Russian thistle, compared to 1 female on live saltbushes, 34 on dead saltbushes, and 2 on Russian thistle (Fig. 3).

Thermal Biology

Eight of 9 locations (88.9%) of lizards were belowground at 20 °C to 23 °C surface temperature (Fig. 4). The lowest surface temperature at which lizards were aboveground was 22.2 °C, and 58.1% of locations were of dark-colored lizards between 22.2 °C and 26.3 °C. The mean surface temperature of locations was 30.82 °C for dark-colored males (range 23.6–39.1 °C) and 29.68 °C for dark-colored females (range 23.6–39.1 °C), and these means were not significantly different ($F_{1,106} = 2.991$, $P = 0.087$). At 23–26 °C, 48.9% of locations of lizards were aboveground, and above 26 °C up to slightly over 45 °C, the percentage of locations aboveground varied between 63.3% and 88.4% (Fig. 4). The highest surface temperature at which lizards were aboveground was 45.4 °C. The percentage of aboveground locations in which lizards were in the shade was significantly positively correlated with surface temperature ($r = 0.895$, $df = 7$, $t = 5.32$, $P < 0.050$). The distribution of surface temperatures of aboveground locations of lizards in the sun differed significantly from that of lizards in the shade ($D = 0.692$, $P = 0.002$), but not between males and females ($D = 0.100$, $P = 1.000$).

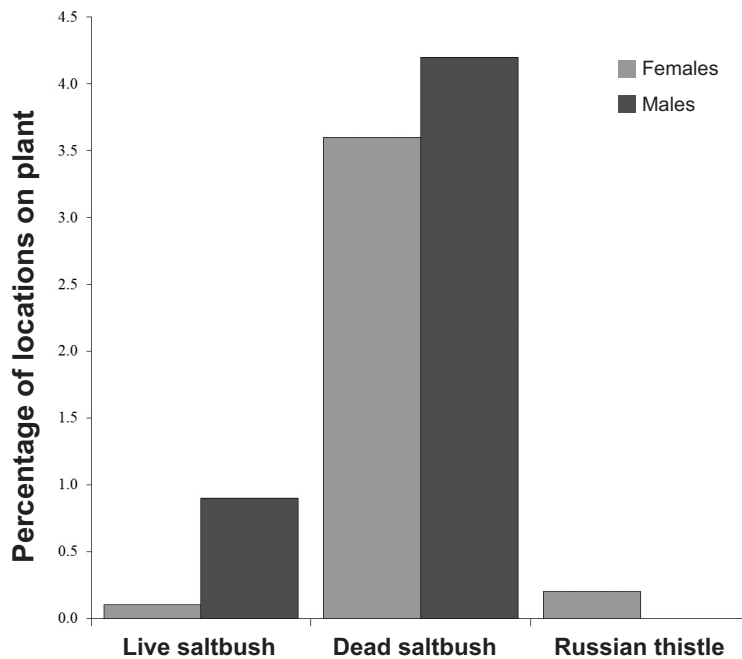


Fig. 3. Percentage of locations of radio-collared Blunt-nosed Leopard Lizards (*Gambelia sila*) found off the ground on live saltbush (*Atriplex* spp.), on burned stems or dead saltbush, or on Russian thistle (*Salsola* spp.), May to August 2003–2004, at the Lokern Natural Area, Kern County, California. Light gray bars are the percentages for females and dark gray bars are the percentages for males.

Average high temperatures on the study site differed significantly by month ($F_{3,7} = 54.27$, $P = 0.001$), with July significantly hotter than all other months ($q = 4.43$ – 17.36 , all P values < 0.05), May significantly cooler than all other months ($q = 9.18$ – 17.36 , all P values < 0.05), and average high temperatures not significantly different between June and August ($q = 3.13$, $P > 0.05$). The temperatures at which the number of locations of active lizards were recorded varied by month, with more lizards found at lower ground temperatures in May and at highest temperatures in July (Fig. 5); these differences were significant ($\chi^2 = 111.42$, $df = 33$, $P < 0.001$). The temperature range of lizards aboveground was significantly higher in July than in all other months (May: $\chi^2 = 72.97$, $df = 11$, $P_{adj} < 0.001$; June: $\chi^2 = 23.93$, $df = 10$, $P_{adj} = 0.023$; August: $\chi^2 = 46.81$, $df = 0$, $P_{adj} = 0.020$). The temperature range of lizards aboveground was significantly higher in June than in May ($\chi^2 = 24.57$, $df = 10$, $P_{adj} = 0.025$) but not higher than in August ($\chi^2 = 8.377$, $df = 9$, $P_{adj} = 0.497$). There was no significant difference between May and August in temperature

ranges of lizards aboveground ($\chi^2 = 16.23$, $df = 9$, $P_{adj} = 0.124$).

On the Elkhorn Plain, the mean cloacal temperature (CT) of active *G. sila* adults was 38.58°C (SE 0.37 , range 30.9 – 42.7°C , $n = 47$) in full sun, 36.82°C (SE 0.53 , range 35.6 – 38.0°C , $n = 4$) in shade, and 34.69°C (SE 0.90 , range 33.1 – 36.2°C , $n = 7$) in burrows. Cloacal temperatures of adults in the sun were significantly related to both air temperature at chest height (ATC; $F_{1,15} = 15.228$, $P = 0.001$, $r^2 = 0.504$) and surface temperature (ST; $F_{1,28} = 17.803$, $P < 0.001$, $r^2 = 0.389$; Fig. 6). The slopes of the equations did not differ significantly ($F_{1,43} = 0.014$, $P = 0.908$), but the intercept of the equation for ground temperature was significantly lower than that for air temperature ($F_{1,43} = 4.101$, $P = 0.049$). The equation relating cloacal temperature to air temperature was $CT = 0.423(ATC) + 26.82$ ($n = 17$), and the equation relating cloacal temperature to surface temperature was $CT = 0.405(ST) + 25.75$ ($n = 30$). At surface temperatures of 26°C and 44°C , the estimated cloacal temperatures of lizards in the sun, using the predictive equation, were 36.28°C and 43.57°C , respectively.

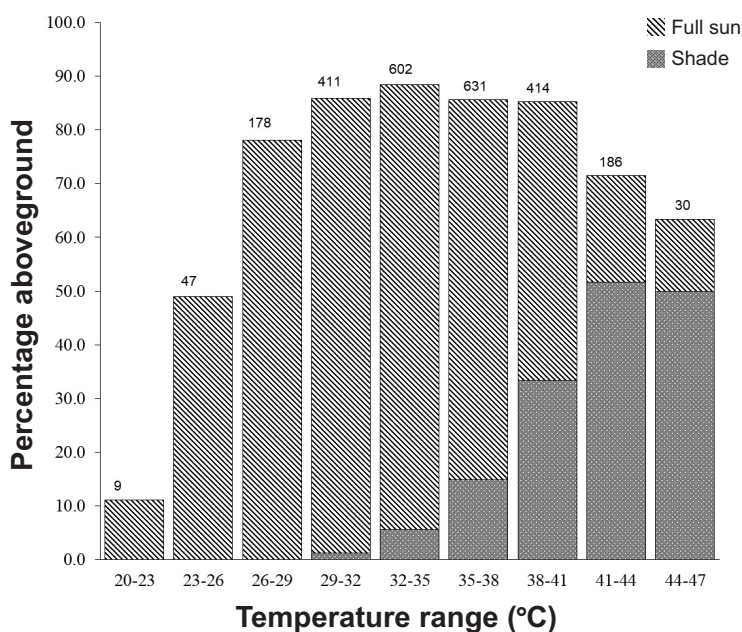


Fig. 4. Percentage of radio-collared Blunt-nosed Leopard Lizards (*Gambelia sila*) found aboveground at differing surface air temperatures from May to August 2003–2004 at the Lokern Natural Area, Kern County, California. The upper temperature in the ranges refers to a temperature just below the integer value (i.e., 23 = 22.9 °C, etc.). Darker shading within bars represents those lizards aboveground that were in the shade of either a live saltbush (*Atriplex* spp.) or the dead branches of a burned saltbush.

On the Lokern study site, mean body temperature of lizards (as measured by transmitter temperature; BTtx) was 38.98 °C (SE = 0.26, range 33.3–42.2 °C, $n = 70$) in full sun, 39.41 °C (SE = 0.27, range 35.5–41.7 °C, $n = 32$) in the shade, and 35.87 °C (SE = 0.61, range 27.8–40.3 °C, $n = 23$) in burrows. The differences among mean BTtx values were significant ($H = 23.68$, $df = 2$, $P < 0.001$), and mean BTtx was significantly lower for lizards in burrows than for those in the sun ($W = 3790.8$, $P < 0.001$) or in the shade ($W = 1155.0$, $P < 0.001$). However, BTtx did not differ significantly between sun and shade ($W = 1710.5$, $P = 0.655$). In shade, BTtx was significantly related to surface temperature ($F_{1,30} = 4.229$, $P = 0.049$, $r^2 = 0.124$; Fig. 6), but not in the sun ($F_{1,68} = 3.025$, $P = 0.087$) or in burrows during the active season ($F_{1,21} = 3.968$, $P = 0.060$). The BTtx of 3 of the lizards that had retreated to end-of-season burrows that were plugged (see below) was significantly related to surface temperature ($F_{1,14} = 14.655$, $P = 0.002$, $r^2 = 0.511$; Fig. 7). The slope of the regression line when the lizards were in plugged burrows did not differ significantly

from that of lizards in the shade ($F_{1,44} = 0.268$, $P = 0.607$), but intercepts were significantly different ($F_{1,45} = 88.795$, $P < 0.001$; Fig. 6). The regression line for BTtx to surface temperature (ST) of *G. sila* in the shade was $BTtx = 0.2026(ST) + 31.478$, and the same regression for lizards in plugged burrows was $BTtx = 0.2720(ST) + 22.316$. At a ground temperature of 26 °C, the estimated body temperature of *G. sila* in the shade is 36.75 °C and in plugged burrows is 29.39 °C, a difference of 7.36 °C. At a ground temperature of 44 °C, the estimated body temperature of *G. sila* in the shade is 40.39 °C and in plugged burrows is 34.28 °C, a difference of 6.11 °C.

End-of-season Burrows

In July and August 2004, radio-tagged *G. sila* began to retreat to burrows, suggesting that the lizards had started their winter period of torpor and inactivity (Table 2). I assumed this for lizards that had been inactive in burrows for 9 or more days. I excavated and removed the transmitters (not temperature sensing) from 2 males and 1 female on 19 July, 9 days after they entered their separate

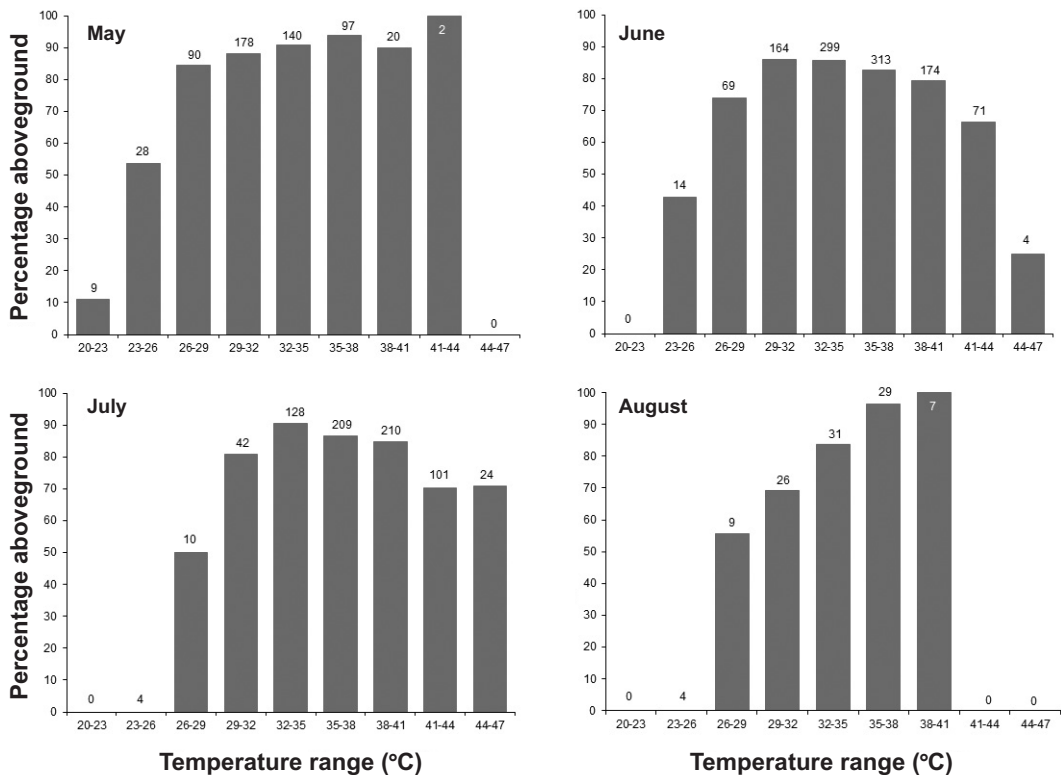


Fig. 5. Percentages of radio-collared Blunt-nosed Leopard Lizards (*Gambelia sila*) found aboveground at differing surface air temperatures by month (May–August) 2003–2004 at the Lokern Natural Area, Kern County, California.

burrows. The males were in lizard-made burrows that were not plugged, and both were in good body condition based on fullness and roundness of the limbs, head, and tail, as well as minor weight change from initial weighing (#4.464: 45.6 g to 49.0 g; #6.246: 60.4 g to 52.0 g). The female was emaciated and in poor condition (weight 58.0 g to 23.0 g). All 3 lizards were in torpor and it took several minutes to arouse them before I released them into different new burrows. Three of the 4 *G. sila* with temperature-sensitive transmitters (TST) retreated to burrows: 2 individuals on 21 July and one on 22 August (Table 2). On 24 July, I found the collar of the fourth lizard with a TST on the ground after I had located the lizard alive and aboveground the day before. I dug lizards #4.129 and #4.149 out of their burrows on 2 September, and #4.169 on 6 September. All were in good condition (#4.129: 48.7 g to 49.0 g; #4.149: 42.2 g to 38 g; #4.169: 49.0 g to 39.0 g). I found these 3 in lizard-made burrows with chambers 17–18 cm

below the ground surface and tunnels 30–73 cm in length (Table 2). In each case, the tunnels were completely backfilled with dirt from the chamber, where the torpid lizards were curled up, to the entrance of the burrow. Although I did not measure them, chambers of each lizard were only a few centimeters larger than their curled-up bodies. I also did not measure tunnel diameters, but I estimated that they were 3–4 cm. The burrow entrances could not be detected due to the dirt plugs.

DISCUSSION

Activity times and surface temperatures at which *G. sila* adults were not in burrows during the active season are similar to those for other diurnal desert lizards (Cowles and Bogert 1944, Brattstrom 1965, Dixon 1967, Pianka and Parker 1972, Bradshaw 1988). A few *G. sila* individuals began emerging from burrows between 0700 and 0800, but the highest percentage of lizards emerged after 0800. Between 0800 and 1400, most lizards

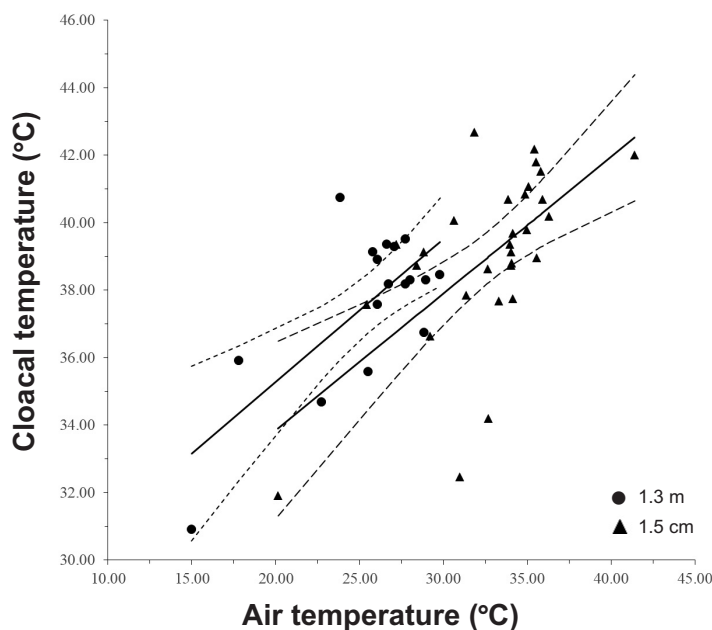


Fig. 6. The relationship of cloacal temperature ($^{\circ}\text{C}$) of Blunt-nosed Leopard Lizards (*Gambelia sila*) to air temperature ($^{\circ}\text{C}$) measured about 1.3 m above the ground (circles, left regression line) and air temperature measured about 1.5 cm above the ground (triangles, right regression line) at Elkhorn Plain, San Luis Obispo County, California. Dashed lines are the 95% confidence limits of the regression lines.

were in the sun, but by the late afternoon, many retreated to surface shade. Most, however, did not retreat to burrows during the hottest times of the day. In comparison, the Long-nosed Leopard Lizard (*G. wislizenii*) in the Great Basin Desert is most active in May and June from 1100 to 1300, with a few lizards active up to 1700. In July and August, *G. wislizenii* is most active from 0800 to 1100 (Parker and Pianka 1976). In western Colorado, only a few *G. wislizenii* were found basking before 0730, but then individuals actively fed until 1230–1300, rested in the shade or in burrows until 1630–1700, and reemerged to bask and forage until sunset (McCoy 1967). The activity times of *G. sila* are similar to those of *G. wislizenii*, although because I followed radio-tagged lizards, I know that most individuals did not retreat to burrows during midday.

I found no differences between *G. sila* males and females in time of activity, use of shade, temperatures when emerging, or other activities. These results are similar to those of Huey and Pianka (2007) for a large number of lizard species. The only difference in behavior that I found between sexes was that males

used live saltbushes as perches more than females did, but both sexes climbed onto stems of dead or burned saltbushes with the same frequency. This difference in use of perch types may be related to live saltbushes being 1 m or more tall, whereas dead bushes were only 10–20 cm above the ground. Both perch types likely kept lizard body temperatures lower than lying on the ground did, thereby affording the possibility of continued prey capture as temperatures increased; however, because males are territorial (Montanucci 1965, Tollestrup 1983), male use of tall perches might additionally confer advantages in guarding territories at high temperatures.

Many of the aboveground locations of *G. sila* were at relatively high temperatures, from 29 $^{\circ}\text{C}$ to above 44 $^{\circ}\text{C}$, which also has been found in other diurnal desert lizards (Brattstrom 1965, Parker and Pianka 1976, Schall 1977, Bradshaw 1988). Adult *G. sila* body temperatures corresponded to ground temperatures across months, and the lizards remained active (not in burrows) at successively higher temperatures into July, the hottest month when adults were active. I found mean body temperatures of lizards in the sun

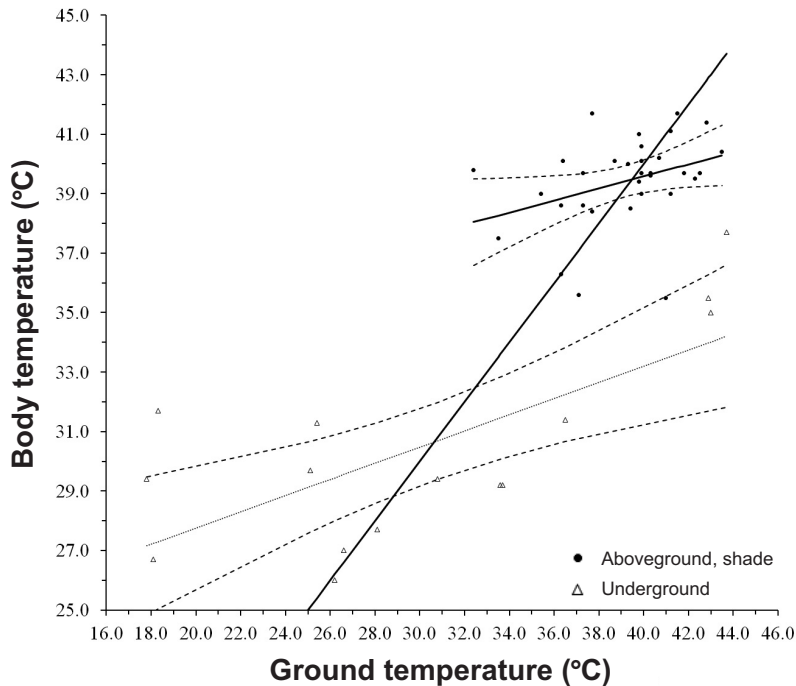


Fig. 7. The relationship of body temperature ($^{\circ}\text{C}$) as measured by the pulse rate of attached temperature-sensitive radio transmitters to air temperature ($^{\circ}\text{C}$) measured about 1.5 cm above the ground for 4 Blunt-nosed Leopard Lizards (*Gambelia sila*) from the Lokern Natural Area, Kern County, California, in the shade during the active season (closed circles, upper regression line) and for 3 *G. sila* underground in their end-of-season burrows that were plugged (open triangles, lower regression line). Dashed lines are the 95% confidence limits of the regression lines. The solid black line without error bars shows where body temperature equals ground temperature.

TABLE 2. Approximate date of retreat underground, qualitative condition of lizard, and architecture of retreat burrows of 6 Blunt-nosed Leopard Lizards (*Gambelia sila*) during 2004 at the Lokern Natural Area, Kern County, California. Depth of burrow refers to depth of burrow underground.

Sex	ID	Date	Condition	Burrow architecture			
				Type	Depth (cm)	Length (cm)	Entrance
M	4.464	10 July	Good	Lizard-built	10	40–50	Open
F	6.213	10 July	Poor: thin	Kangaroo rat	15	20	Open
M	6.246	10 July	Good	Lizard-built	15	40	Open
M	4.129	21 July	Good	Lizard-built	18	73	Plugged
M	4.149	21 July	Good	Lizard-built	17	45	Plugged
M	4.169	22 Aug.	Good	Lizard-built	18	30	Plugged

to be 38–39 $^{\circ}\text{C}$, no matter whether I measured cloacal temperatures with a glass thermometer or examined transmitter temperatures. Brattstrom (1965) found that cloacal temperatures for 13 *G. sila* ranged from 35 $^{\circ}\text{C}$ to 41 $^{\circ}\text{C}$, with a mean of 38.0 $^{\circ}\text{C}$. In Nevada, the body temperature of *G. wislizenii* spanned 32.0–42.5 $^{\circ}\text{C}$ with a mean of 39.0 $^{\circ}\text{C}$ (Tanner and Krogh 1974). The cloacal temperatures I measured were significantly related to both

elevated air temperature and surface temperature, and when the surface temperature was 44 $^{\circ}\text{C}$, the estimated cloacal temperature of lizards in the sun was 43.57 $^{\circ}\text{C}$. Most diurnal desert lizards have high body temperatures when active (Dixon 1967, Pianka and Parker 1972, Muth 1977, Schall 1977, Bradshaw 1988), and these temperatures are higher than preferred body temperatures in a thermal gradient (Pianka and Parker 1972, Schall

1977). Also, although high, these temperatures never reach levels that would induce panting (indicating stress) or critical thermal maxima that would be lethal (Bradshaw 1988). Schall (1977), working on 5 species of whip-tail lizards (*Aspidoscelis* spp.), postulated that because these widely foraging whiptails are diurnal and live in hot environments, the lizards are selected to have high body temperatures to reduce costs of thermoregulation and to support quick physiological reactions that assist in foraging and escaping predators. This also seems to apply to *G. sila*, which hunts beetles, grasshoppers, and other fast-moving invertebrates, and also must escape snakes and diurnal birds of prey (Montanucci 1965, Germano and Brown 2003, Germano et al. 2015).

I found a significant relationship between transmitter temperature and surface temperature when lizards were in the shade. This relationship estimates a body temperature of 40.39 °C for lizards in the shade when surface temperatures (beyond the shade) are 44 °C. *Gambelia sila* reduces its internal temperatures by >3 °C by retreating to shade while still aboveground. The relationship between transmitter temperature and ground temperature for lizards that were underground was nearly significant ($P = 0.060$). If the P value for significance is slightly relaxed, the regression relationship estimates the body temperature of *G. sila* in burrows as 37.72 °C at a ground temperature of 44 °C, a drop of >6 °C. This result highlights the point that *G. sila*, like many other desert lizards, has been selected to remain at a high body temperature and will retreat to shade aboveground to maintain sublethal temperatures even though it would be cooler underground. This thermoregulatory behavior may allow for continued prey capture and mating activities that would be precluded if lizards went underground.

The characteristics of burrows in which *G. sila* retreat for the year have not previously been available. Three lizards that became inactive on 10 July did not plug their burrows, although the 3 males that retreated in late July or early August did. The earlier retreating lizards might only have been down temporarily, even toward the tail end of the active season, yet they had not been active for 9 d and were in deep torpor when excavated. Of the 6 *G. sila* that seemed to have

retreated to winter burrows, only the female did not use a lizard-made burrow. She used a kangaroo rat (*Dipodomys* sp.) burrow, and because she was in very poor condition, she may not have had the energy to dig her own burrow. The later retreaters completely plugged their burrows. Based on their temperature-sensitive radio transmitters, the body temperatures of these lizards increased as surface temperatures increased during the day, but temperatures of lizards in burrows were always 6–7 °C lower than lizards in the shade and the magnitude of difference was even larger compared to lizards in the sun. Brattstrom (1965) found one *G. sila* under a rock with a body temperature of 26.0 °C and a surface temperature of 24.4 °C, and one under a board at 14.0 °C when the surface temperature was 14.0 °C. This finding illustrates that the thermal inertia and insulating properties of the earth surrounding burrows buffer the temperatures of the burrow chambers from reaching the high and low (including freezing) aboveground surface temperatures.

From a conservation and management standpoint, the data I have presented indicate that the current survey protocol for *G. sila* surveys (California Department of Fish and Game, Approved survey methodology for the Blunt-nosed Leopard Lizard, May 2004) for surveys for many projects in habitats where the lizard may occur does not adequately account for the time *G. sila* becomes active aboveground and is too restrictive for high temperatures at which lizards are active. The protocol states that surveys must be done only after sunrise when surface air temperatures are between 25 °C and 35 °C and that surveys must end by 1400 or when surface air temperatures exceed 35 °C. Sunrise within the range of the lizard occurs between 0542 and 0617 from 1 May to 15 August. Even on the hottest days, only a few *G. sila* were aboveground before 0800, and none were aboveground before 0720. Thus, the best times to start surveys is after 0800 and after surface air temperatures are >26 °C. I found that a majority of lizards were active in the sun up to 41 °C and that some lizards were still visible aboveground up to about 45 °C, although many were in the shade of bushes. Thus, surveys can be done up to a surface temperature of 41 °C, because many lizards are still active at that temperature.

Sinervo et al. (2010) have argued that climate change will increase environmental

temperatures enough that many lizard species, even desert species, will reach their upper thermal limits more often, reducing the time when they are active. These changes, in turn, will result in reduced food intake and lower reproduction and will likely lead to extinction. Clusella-Trullas and Chown (2011) noted that Sinervo et al. (2010) did not account for varying frequency distributions of operative temperatures (T_e) of diurnal lizards, and that estimates of restricted activity due to temperatures above preferred body temperatures (h_r) are likely in error. Sinervo et al. (2011) responded to this criticism by showing that, at least for some lizard families, the variances in frequency distributions of operative temperatures are small compared to forecasted increases in environmental temperatures. Even if some activity time is foreshortened by increased air temperatures, it has not been demonstrated that lizards require the time daily at which they operate now to maintain populations. Also, despite these modeling efforts, the flexible nature of lizard behavior (compared to their relatively static morphological and physiological traits) might confer a buffer to these projected increases in air temperature, at least for some species. A lacertid species in the Namibian Desert behaviorally regulates its body temperature below its high thermal preference in the summer, thus avoiding critical thermal maximum (Kirchhof et al. 2017). The range of this species has not contracted since the 1960s even though there have been increases in air temperature, although the authors warn that this could change in the future if temperatures increase further (Kirchhof et al. 2017). In the case of *G. sila*, although lizards seek shade when temperatures rise during the day, most of the time they do not enter burrows, but rather seek the shade of shrubs. Also, *G. sila* are not active for several hours of daylight in the cool mornings under current thermal regimes. I speculate that this species will become active earlier after sunrise to compensate for any lost active time later in the day. In southern Oregon, some *G. wislizenii* individuals voluntarily become hypothermic by staying on shrubs overnight, which can lengthen foraging times the next day (Nicholas 1978; cited in Huey 1982). Because *G. sila* uses shrubs similarly, it may be able to behaviorally cope with a rise in air temperatures and not compromise foraging or mating

activity. Also, despite the loss of habitat, which led to the endangered status of *G. sila* originally and continues to be the greatest threat to its recovery (USFWS 1998), climate change potentially will increase suitable habitat for *G. sila* over the present climate regime (Stewart et al. 2019).

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