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

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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

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(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,
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 above-ground. 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.
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 Elk-horn 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
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 $G. \text{sil}a$ 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 ($r = 0.885, df = 7, t = 5.32, P < 0.050$). 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 ($D = 0.100, P = 1.000$).

<table>
<thead>
<tr>
<th>Month</th>
<th>$r$</th>
<th>$n$</th>
<th>$t$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
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<td>May</td>
<td>0.332</td>
<td>564</td>
<td>8.34</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>June</td>
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<td>921</td>
<td>19.0</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>July</td>
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<td>638</td>
<td>22.3</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>August</td>
<td>0.561</td>
<td>100</td>
<td>6.20</td>
<td>&lt;0.001*</td>
</tr>
</tbody>
</table>

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 ($\alpha = 0.05$).
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 $CT = 0.423(\text{ATC}) + 26.82$ ($n = 17$), and the equation relating cloacal temperature to surface temperature was $CT = 0.423(\text{ATC}) + 26.82$ ($n = 17$). 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.
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...
burrows. The males were in lizard-made bur-
rows 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 dif-
ferent 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 Sep-
tember. 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 tun-
nels 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 dur-
ing 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
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 °C to above 44 °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 progressively higher temperatures into July, the hottest month when adults were active. I found mean body temperatures of lizards in the sun

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Fig. 6. The relationship of cloacal temperature (°C) of Blunt-nosed Leopard Lizards (*Gambelia sila*) to air temperature (°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.
to be 38–39 °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 °C to 41 °C, with a mean of 38.0 °C. In Nevada, the body temperature of G. wislizenii spanned 32.0–42.5 °C with a mean of 39.0 °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 °C, the estimated cloacal temperature of lizards in the sun was 43.57 °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

![Graph showing the relationship between body temperature and ground temperature.](image)

**Fig. 7.** The relationship of body temperature (°C) as measured by the pulse rate of attached temperature-sensitive radio transmitters to air temperature (°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.

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<thead>
<tr>
<th>Sex</th>
<th>ID</th>
<th>Date</th>
<th>Condition</th>
<th>Type</th>
<th>Depth (cm)</th>
<th>Length (cm)</th>
<th>Entrance</th>
</tr>
</thead>
<tbody>
<tr>
<td>M</td>
<td>4.464</td>
<td>10 July</td>
<td>Good</td>
<td>Lizard-built</td>
<td>10</td>
<td>40–50</td>
<td>Open</td>
</tr>
<tr>
<td>F</td>
<td>6.213</td>
<td>10 July</td>
<td>Poor: thin</td>
<td>Kangaroo rat</td>
<td>15</td>
<td>20</td>
<td>Open</td>
</tr>
<tr>
<td>M</td>
<td>6.246</td>
<td>10 July</td>
<td>Good</td>
<td>Lizard-built</td>
<td>15</td>
<td>40</td>
<td>Open</td>
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<tr>
<td>M</td>
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<td>21 July</td>
<td>Good</td>
<td>Lizard-built</td>
<td>18</td>
<td>73</td>
<td>Plugged</td>
</tr>
<tr>
<td>M</td>
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<td>21 July</td>
<td>Good</td>
<td>Lizard-built</td>
<td>17</td>
<td>45</td>
<td>Plugged</td>
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<tr>
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<td>22 Aug.</td>
<td>Good</td>
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<td>18</td>
<td>30</td>
<td>Plugged</td>
</tr>
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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 sur- veys 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 ($h_p$) 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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LITERATURE CITED


