

Thermal ecology of the federally endangered blunt-nosed leopard lizard (*Gambelia sila*)

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Recognizing how climate change will impact populations can aid in making decisions about approaches for conservation of endangered species. The blunt-nosed leopard lizard (*Gambelia sila*) is a federally endangered species that, despite protection, remains in extremely arid, hot areas and may be at risk of extirpation due to climate change. We collected data on the field-active body temperatures, preferred body temperatures and upper thermal tolerance of *G. sila*. We then described available thermal habitat using biophysical models, which allowed us to (i) describe patterns in lizard body temperatures, microhabitat temperatures and lizard microhabitat use; (ii) quantify the lizards' thermoregulatory accuracy; (iii) calculate the number of hours they are currently thermally restricted in microhabitat use; (iv) project how the number of restricted hours will change in the future as ambient temperatures rise; and (v) assess the importance of giant kangaroo rat burrows and shade-providing shrubs in the current and projected future thermal ecology of *G. sila*. Lizards maintained fairly consistent daytime body temperatures over the course of the active season, and use of burrows and shrubs increased as the season progressed and ambient temperatures rose. During the hottest part of the year, lizards shuttled among kangaroo rat burrows, shrubs, and open habitat to maintain body temperatures below their upper thermal tolerance, but, occasionally, higher than their preferred body temperature range. Lizards are restricted from staying in the open habitat for 75% of daylight hours and are forced to seek refuge under shrubs or burrows to avoid surpassing their upper thermal threshold. After applying climatic projections of 1 and 2°C increases to 2018 ambient temperatures, *G. sila* will lose additional hours of activity time that could compound stressors faced by this population, potentially leading to extirpation.

Key words: *Gambelia sila*, thermal ecology, behavioral thermoregulation, climate change, hours of restriction, thermoregulatory accuracy

Editor: Steven Cooke

Received 23 July 2019; Revised 23 January 2020; Editorial Decision 2 February 2020; Accepted 2 February 2020

Cite as: Ivey KN, Cornwall M, Crowell H, Ghazian N, Nix E, Owen M, Zuliani M, Lortie CL, Westphal M, Taylor E (2020) Thermal ecology of the federally endangered blunt-nosed leopard lizard (*Gambelia sila*). *Conserv Physiol* 8(1): coaa014; doi:10.1093/conphys/coaa014.

Introduction

As anthropogenic climate change accelerates, so has the urgency for studies examining how rising temperatures will impact sensitive species. By 2050, up to 18% of species worldwide will be extinct (Thomas *et al.*, 2004; Urban *et al.*, 2015), with human-caused land use changes having the potential to further increased extinction risk (Powers and Jetz, 2019). The actions we take now in terms of habitat management may mitigate the potential impacts of climate change on endangered species. Because ectotherms depend on ambient temperatures for their normal physiological processes (Stevenson, 1985; Walther *et al.*, 2002), they are very sensitive to thermal changes in their habitats (Sinervo *et al.*, 2010; Buckley *et al.*, 2015). This is especially true for ectotherms living in extremely hot environments where they are thermally constrained (Grant and Dunham, 1988; Bashy and Dunham 1997; Zamora-Camacho *et al.*, 2016) and have limited plasticity that would allow them to survive with further warming (Gunderson and Stillman, 2015). Because of their abundance, ease of study and diversity in extremely hot environments worldwide, lizards have become model organisms for studies of thermal tolerance, with important implications for conservation biology. As many as 30% of all lizard populations could be extinct by 2080 (Sinervo *et al.*, 2010), and it is unclear whether thermoconforming lizards or heliothermic (sun-basking) lizards will fare worse (Sinervo *et al.*, 2010).

Habitat heterogeneity is important to lizards and other ectotherms as it allows them to exploit behavioural thermoregulation to maintain a body temperature close to their preferred body temperature (Sears *et al.*, 2011; Carroll *et al.*, 2016). Temperatures on the surface of the ground exposed to the sun often exceed the thermal tolerance of lizard species (Sunday *et al.*, 2014), and so the availability of shade is important for thermoregulation (Kearney *et al.*, 2009). Notably, refugia provide refuge not only from predators but also from thermally unsuitable conditions (Bradshaw and Main, 1968; Souter *et al.*, 2007; Pike and Mitchell, 2013; Lortie *et al.*, 2015; Moore *et al.*, 2018; Suggitt *et al.*, 2018). Vegetation may assist animals with thermoregulation by providing them with a complex mosaic of thermal and radiative properties on the surface of the ground (Carroll *et al.*, 2016; Milling *et al.*, 2018). Plants are important to the thermoregulation of lizards inhabiting extremely hot environments because they allow lizards to be surface active while protecting the lizards from intense solar radiation. (e.g. Porter *et al.*, 1973; Bauwens *et al.*, 1996). This includes, but is not limited to, essential activities like territory defence, mate guarding and feeding.

The blunt-nosed leopard lizard (*Gambelia sila*) is a federally endangered species with isolated populations in the San Joaquin Valley and the southeastern Carrizo Plain in California (U.S. Fish and Wildlife Service, 1998; Germano and Rathbun, 2016; IUCN, 2017), an area with extremely hot and arid conditions. Since the 1960s, the species' range

has decreased by 85% due to agriculture, oil exploration and invasive grasses (Germano *et al.*, 2001; Filazzola *et al.*, 2017). The active season for adults is limited to as little as 2.5 months in the spring and early summer (Germano *et al.*, 1994), after which time they estivate and then transition directly into hibernation. It is therefore likely that *G. sila* is already clinging to existence in a thermally stressful environment, and evaluation of the thermal ecology of this species is likely to provide managers and researchers with valuable information about climate change mitigation efforts for this species (Germano, 2019). A significant amount of the remaining habitat occupied by *G. sila* is dominated by the Mormon tea shrub, *Ephedra californica* (Stout *et al.*, 2013), which creates spotty microhabitats that are cooler and more humid than the open ground (Filazzola *et al.*, 2017). Lizards are regularly found in the shade of these shrubs, especially in the afternoon when temperatures are highest (Westphal *et al.*, 2018; Germano, 2019). Given that the habitats occupied by *G. sila* tend to be structurally simple (i.e. lizard microhabitat choices are limited to the open desert floor, rodent burrows and *Ephedra* shrubs), modelling the thermal ecology of *G. sila* provides an excellent opportunity to quantify the importance of these microhabitats, both currently and as the climate warms.

In this study, we describe the thermal ecology of a population of *G. sila* in the southeastern Carrizo Plain over the course of one active season with the goals of (i) quantifying the daily and seasonal body temperatures of lizards, (ii) describing how lizards behaviourally use available microhabitats, (iii) determining their thermoregulatory accuracy, (iv) calculating the number of hours they are currently restricted to shade and/or burrows due to extreme heat and (v) projecting how these values are likely to be impacted by climate change during this century. Given that the only above-ground shade available to lizards at this site is provided by sparsely distributed *Ephedra* shrubs, we also explicitly test the hypothesis that shrubs currently act as thermal buffers that allow the lizards to remain active above ground longer than they would if there were no shrubs.

Methods

Field site

Our study site is located within the Elkhorn Plain (35.117998°–119.629063°) in the Carrizo Plain National Monument, California, USA. This area is characterized by extremely harsh, arid summers (average high 30–40°C) and cool winters (average low 5–9°C, Germano and Williams, 2005; Raws USA Climate Archive, 2019). This site is part of the San Joaquin Desert (Germano *et al.*, 2011), which in modern times has been frequently misclassified as a grassland prairie, despite early European explorers describing the landscape as lacking dominant annual or perennial grasses (D'Antonio *et al.*, 2007; Schiffman, 2007; Minnich, 2008). When

temperatures rise in this area, the vegetation dies off in early May, leaving the ground barren and resembling that of an arid desert with occasional small saltbush plants (Minnich, 2008) and in some areas, including our site, sparsely distributed *Ephedra* shrubs. The area is dominated by giant kangaroo rat (*Dipodomys ingens*) precincts with extensive burrow networks. Our study spanned one active season of *G. sila* (May–July 2018). We obtained ambient temperature data from a weather station (Cochora Ranch, station ID: CXXC1) 3.7 km due east of the field site.

Study species and field monitoring

Adult *G. sila* ($N = 30$) were captured by hand-held lasso in early May 2018. Snout–vent length (SVL, ± 0.1 cm), mass (Pesola® 50–100 g precision scale, ± 0.5 g) and sex were recorded upon capture (Table S1). Females were palpated for follicles and recorded as gravid or not. Lizards were fitted with VHF temperature-sensitive radio-transmitter collars (Holohil model BD-2T, Holohil Systems Ltd, Carp, ON, Canada) following the methods of Germano and Rathbun (2016). The transmitters were epoxied to nickel-plated ball chain collars, which were fitted around the lizards' necks, with whip antennas (16 cm) extending dorsally from the collars. Lizards were released the same day of capture. Following release, lizards were tracked one to three times per day using a VHF receiver and Yagi antenna (R-1000 Telemetry Receiver, Communications Specialists, Inc., Orange, CA, USA), resulting in an average of 55 observations on each lizard over the active season. Behavioural observations, microhabitat (open desert floor, under shrub or in burrow), GPS location and time of day were recorded at each tracking event. At the end of the study, lizards were recaptured by lasso or excavated from burrows and collected for measurement of preferred body temperature and thermal tolerance (see below). Collars were then removed, SVL and mass data were recorded again and lizards were released at their sites of capture, at which time they entered estivation for the remainder of the summer.

Field active body temperature (T_b) and microhabitat use

We continually recorded the temperatures of the radio-transmitters as the field active lizard body temperature (T_b) using a Telonics TR-5 receiver with data acquisition system (Telonics Option 320) and 10-ft-tall omni antenna (Telonics model RA-6B). We programmed the system to log the interpulse intervals of the transmitters about every 10 min and used manufacturer-provided calibration equations to convert interpulse interval to temperature. This resulted in a total of $\sim 90\,000$ T_b points for the 30 lizards spanning their active season from May to July. Because radio-transmitters were external (collars), it is possible that they could heat more rapidly than the lizard's core actual T_b , especially when lizards are in the sun. This may lead to a slight overestimate of lizard T_b than if core T_b had been collected, which is not

possible with external radio-transmitters. Data were checked manually for aberrant points, which were removed. We used an ANCOVA to test whether SVL, mass, sex or gravidity affected mean T_b and a repeated measures ANOVA with time of day (daytime or night time), month, the interaction between time of day and month and lizard ID as a random effect, to analyze how T_b changed over the active season (May–July), and Tukey post hoc tests to compare monthly night time temperatures or monthly daytime temperatures. We also used field-active T_b data to calculate the field-active voluntary maximum T_b (VT_{max}), or the average maximum daily T_b , which presumably occurred when the lizard was active above ground exposed to solar radiation (Brattstrom, 1965), to use in the activity restriction analysis (see below). To test the hypothesis that lizard microhabitat differed by month, we calculated an initial Pearson's chi-square statistic from the observed data. We then ran a permutation test by shuffling the observations across months and computing a chi-square statistic for each permutation. This analysis was performed in R (R Core Team, 2017), and all other analyses were performed in JMP® (v. Pro 14).

Preferred body temperature (T_{set}) and thermoregulatory accuracy (d_b)

At the end of the study (mid-July), lizards were collected from the field site and brought to a field station to collect data on their preferred body temperature range (T_{set}) in a thermal gradient. The gradient consisted of sand substrate divided into three lanes ($250 \times 20 \times 25$ cm each) separated by wood dividers so lizards could not see lizards in neighbouring lanes. One end of the gradient was heated to 47°C with a closed-circuit 4 gallon water heater (Stiebel Eltron model no. SHC4, Germany), and the other end was cooled to 10°C with a closed-circuit 400-L water cooler (ActiveAQUA Refrigerateur model no. AACH10, Petaluma, CA, USA). Water circulated under the gradient in insulated pipes from the heated side to the cold side to create the thermal gradient. Thermocouples (model 5SRTC-TT-K-40-72, Omega Engineering, UK) were inserted into the lizard's cloacae and held in place by medical tape wrapped around the base of the tail. The thermocouples recorded T_b every 5 min on a data logger (model RDXL4SD, Omega Engineering, Egham, Surrey, UK). Lizards were placed in the centre of the gradient and left undisturbed for 3 h (the first 2 h were used as an acclimation period, and the final hour was used to determine T_{set}). We designated T_{set} as the 25–75% interquartile range of the final hour T_b . Data collection for the 30 lizards ran continually day and night over several days to minimize the amount of time the lizards were kept in captivity before release. We excluded T_{set} data for three lizards from the analysis (10.6 , 14.3 , 18.2°C) because they were >2 SD away from the median and were likely from lizards that failed to actively thermoregulate within the gradient in the time allotted. We used an ANCOVA to test the effects of sex, SVL, mass, capture method (lasso or excavation) and time of day on median T_{set} . We calculated lizard thermoregulatory accuracy (d_b) by subtracting the mean T_{set}

IQR from each instance of T_b (Hertz *et al.*, 1993), then averaged all d_b values for a single lizard within each 1-h period per day from 0700 to 1900, then averaged all d_b by hour of day to create average hourly d_b values. Either very high positive or very low negative values of d_b represent poor accuracy (i.e. the field-active T_b are much higher or lower than T_{set}), and zero represents perfect accuracy.

Upper thermal tolerance (T_{pant})

The upper thermal tolerance of lizards is typically measured as a loss of righting response or the onset of muscular spasms in response to high temperature, which represents the critical thermal maximum (CT_{max}), or the high temperature at which a lizard loses muscular coordination and will die if heated further (Cowles and Bogert, 1944; Larson, 1961; Prieto and Whitford, 1971; Shea *et al.*, 2016). At T_b slightly below the CT_{max} , lizards begin gaping and panting, presumably to increase evaporative cooling rates (Dawson and Templeton, 1963; Heatwole *et al.*, 1973; Tattersall *et al.*, 2006). Given that *G. sila* is a federally endangered species, we chose to use their panting threshold (T_{pant}) as a conservative measure of their upper thermal tolerance so that we did not expose lizards to excessively stressful or potentially fatal high temperatures. To measure T_{pant} , we used a Cal Poly-engineered device, the Gas Analysis Temperature Oxygen Regulation System (GATORS). Lizards were fitted with cloacal resistance thermometers, heated at 1°C ambient temperature per minute in individual temperature-controlled chambers (18 cm length, 4 cm diameter), observed for panting behaviour (open mouth and rapid thoracic compression), then promptly removed and cooled. T_{pant} was recorded immediately following collection of T_{set} data. We used an ANCOVA to test the effects of sex, SVL, mass, capture method (lasso or excavation) and time of day on T_{pant} .

Biophysical models and microhabitat temperatures

We used biophysical models to model the ranges of temperatures within microhabitats throughout the course of a day a lizard would experience if it were behaviourally neutral to, or non-thermoregulating within, the environment. Models ($N=18$) consisted of 1" (2.5 cm) diameter copper pipes, welded with a copper female end on one side and a male end on the other. A Thermochron iButton (DS1921G-F5) programmed to record temperature every 10 min and coated in PlastiDip was suspended in the centre of each pipe by a 3D-printed plastic insert to avoid contact with the pipe walls, then pipes were filled with water (Dzialowski, 2005), and PVC caps were screwed onto the male copper ends. Models were fitted with two 3.8-cm 'legs' made from copper wiring to prop models above ground on one end, mimicking a lizard propped up on its front legs. Biophysical model temperatures were validated by comparing internal temperatures to those of a preserved lizard over the course of 120 min of heating in the sun (models were continually

within $\pm 1^\circ\text{C}$ of the lizard). Models were deployed from July 1–19 (a very hot period) in three different microhabitats: on the desert floor exposed to the sun (open, $N=6$), in the shade under *Ephedra* shrubs (shrub, $N=6$), and ~ 1 m inside giant kangaroo rat burrows (burrow, $N=6$). Models in burrows did not have legs to mimic lizards lying prone on the burrow floor. We compared the mean hourly temperatures of the three microhabitats during *G. sila* activity hours (0700–1900) using a two-way ANOVA followed by a Tukey–Kramer post hoc test.

Activity restriction

We used data from the biophysical models along with T_{pant} , VT_{max} and T_{set} data to calculate the activity constraint or hours of restriction (h_r), or the number of hours that a lizard could not be active in a given microhabitat because its T_b would be too high, in several ways:

- (i) *Basking restriction*: the average number of hours per day that lizards are currently restricted from continually basking in the open and are confined to burrows or shade because temperatures of biophysical models in the open exceed T_{pant} , VT_{max} or T_{set} (we calculated hours of restriction separately for each variable).
- (ii) *Above ground restriction*: the average number of hours per day that lizards are currently restricted from remaining active above ground and are confined to burrows because temperatures of biophysical models in the open or in the shade exceed T_{pant} , VT_{max} or T_{set} .
- (iii) *Total restriction*: the average number of hours per day that temperatures of biophysical models in all microhabitats exceed T_{pant} , VT_{max} or T_{set} .

Climatic projections

To assess how h_r might change in the future due to consequences of anthropogenic climate change, we used Cal-Adapt's representative concentration pathway (RCP) climate scenario 4.5 and 8.5 (California Energy Commission, 2019). RCP 4.5 is a conservative scenario which predicts a steady decline following peak carbon emissions in 2040. RCP 8.5 is a worst-case scenario in which carbon emissions continue throughout the 21st century, peaking in 2050 and plateauing around 2100. Using the 'modeled projected annual mean' tool, we identified the years where the annual average temperatures in the Elkhorn Plain are projected to increase 1 and 2°C from the 2018 average. To make our predictions, we added a 1°C increase unilaterally across the 2018 biophysical model data. We projected how each h_r variable would be affected by climate change by adding 1 and 2°C to current biophysical model temperatures (+1°C h_r and +2°C h_r). Note that temperatures inside burrows, under shrubs and out in the open are unlikely to actually increase at the same rates, but this method provides us with a coarse estimate as to how h_r might change with warming climates (Brusch *et al.*, 2016).

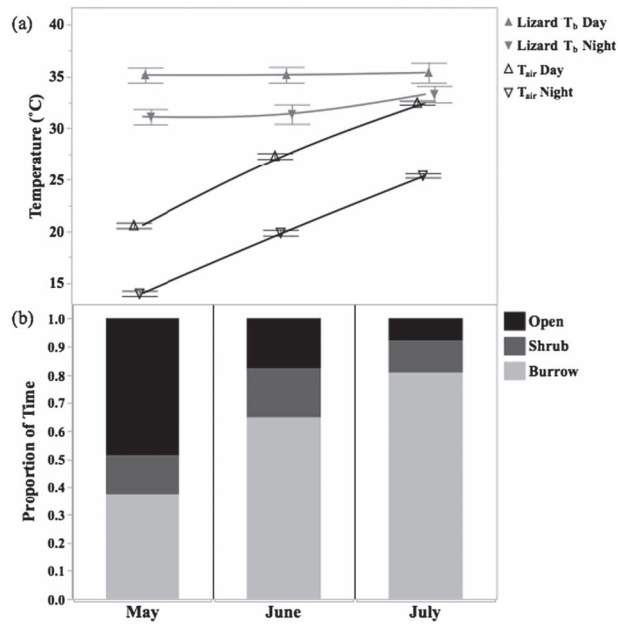


Figure 1: Monthly body and ambient temperatures and microhabitat selection by *Gambelia sila* ($N = 30$) over the course of their active season (May–July 2018). (a) Both daytime and night-time ambient temperatures (T_{air}) increased as the season progressed, but lizard T_b remained constant during daytime hours as they thermoregulated. Night-time T_b increased in July. Values shown are means ± 1 SEM. (b) As ambient temperatures increased, lizards increased the proportion of time spent in burrows and decreased the proportion of time spent in the open during daylight hours. Shrubs therefore represented an increasing proportion of the above-ground microhabitat use as temperatures increased over the season

Results

Field active body temperature (T_b) and microhabitat use

Mean T_b was not impacted by sex ($F_1 = 0.91$, $P = 0.35$) or by initial SVL ($F_1 = 0.10$, $P = 0.75$), mass ($F_1 = 0.29$, $P = 0.59$). Within female lizards, T_b did not differ between gravid and non-gravid lizards ($F_1 = 0.16$, $P = 0.70$). Monthly mean daytime and night-time ambient temperatures increased from May to June to July, as expected, with daytime average temperatures consistently about 6–8°C higher than night-time temperatures (Fig. 1a). Despite the dramatic increase in ambient temperatures over the course of the active season, lizard T_b did not vary across each month ($F_{123.6} = 2.0$, $P = 0.14$), and there was no interaction between month and time of day ($F_{122.9} = 1.26$, $P = 0.29$). As expected, average monthly mean daytime T_b of lizards was significantly higher than night-time T_b ($F_{122.9} = 38.6$, $P < 0.001$). Tukey post hoc tests showed that night-time T_b increased significantly in July compared to May and June, presumably because burrow temperatures increased. The calculated VT_{max} of *G. sila* was $40.4 \pm 0.8^\circ\text{C}$.

As ambient temperatures increased, we observed a concomitant increase in burrow use and decrease in time spent in the open microhabitat during daylight hours (Fig. 1b). In the permutation independence test, the chi-square test statistic computed from the original data was 250. Of the 5000 independent permutations performed, our initial statistic was only exceeded three times, resulting in a permutation P value of 0.0006, showing that microhabitat selection significantly differed by month.

Average daily T_b of *G. sila* during an extremely hot part of their active season (1–19 July 2019) is shown in Fig. 2, along with T_{set} range, T_{pant} and T_e in the three microhabitats (results below).

Preferred body temperature (T_{set}) and thermoregulatory accuracy (d_b)

The median preferred body temperature of *G. sila* is $34.1 \pm 1.2^\circ\text{C}$, with a T_{set} range of 32.3 ± 1.2 – $37.5 \pm 1.1^\circ\text{C}$ (Fig. 2). There was no significant effect of sex ($F_1 = 3.93$, $P = 0.08$), SVL ($F_1 = 0.02$, $P = 0.90$), mass ($F_1 = 0.26$, $P = 0.62$), capture method ($F_1 = 0.55$, $P = 0.47$) or time of day ($F_4 = 1.10$, $P = 0.41$) on T_{set} . Before 9 am, d_b values were negative because lizard T_b was lower than T_{set} , as even burrows are too cool for lizards to achieve T_{set} at night and early morning (Fig. 3). After about 1100, d_b values become positive as lizard T_b often exceeded T_{set} , especially from about 1400 to 1900 (see Fig. 3).

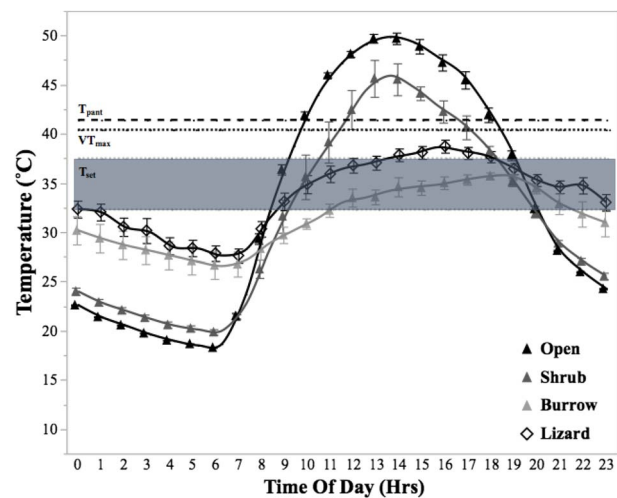


Figure 2: Average daily temperatures of biophysical models in three microhabitats ($N = 6$ each) and *Gambelia sila* body (T_b) temperatures ($N = 30$) during an extremely hot part of their active season (1–19 July 2019). Temperatures above ground (open and shrub) regularly exceeded the upper thermal tolerance (T_{pant}), whereas temperatures in burrows were most often within lizard preferred body temperature (T_{set}) range. Average maximum voluntary body temperature (VT_{max}) did not exceed T_{pant} . Lizards maintained T_b within T_{set} for most of the daylight hours, and lizard T_b never exceeded T_{pant} . Error bars represent ± 1 SEM

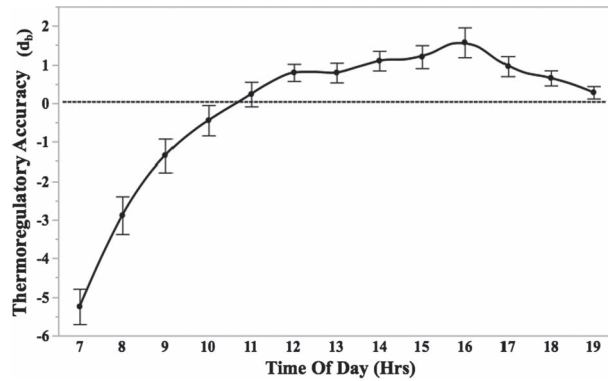


Figure 3: Average thermoregulatory accuracy (d_b) of *Gambelia sila* ($N = 30$) over the course of the active season (May–July 2018) plotted against time of day from 0700–1900. Error bars represent ± 1 SEM. Values at zero (dashed line) indicate that the lizard is thermoregulating within the T_{set} range. As values move away from zero in either direction, the accuracy of thermoregulation decreases

Upper thermal tolerance (T_{pant})

There was no effect of sex ($F_1 = 2.81$, $P = 0.11$), SVL ($F_1 = 0.01$, $P = 0.92$), mass ($F_1 = 2.27$, $P = 0.15$) or capture method ($F_1 = 1.39$, $P = 0.26$) on T_{pant} . Mean T_{pant} was $41.4 \pm 0.2^\circ\text{C}$ (Fig. 2). Given that the true upper thermal threshold (CT_{max}) is usually several degrees higher than T_{pant} (e.g. Heatwole *et al.*, 1973; Shea *et al.*, 2016), the CT_{max} of *G. sila* is probably in the mid 40°C range.

Biophysical models

Based on data from biophysical models, hourly day-time (0700–1900) temperature from 1 to 19 July 2019 varied significantly among microhabitats ($F_{14,38} = 11.07$, $P < 0.0001$), with temperatures in the open highest, under shrubs intermediate and in burrows lowest (Fig. 2).

Restricted activity time

Currently, during the hottest time of the active season, *G. sila* are restricted from continually basking in the sun for 8–9 h a day (Fig. 4), forcing them into burrows or under shrubs because temperatures of biophysical models in the direct sun exceed all three thermal variables (T_{pant} , VT_{max} and T_{set}). Even the ground beneath shrubs is above T_{pant} for 5 h a day, where lizards are restricted to using burrows only. Currently, mean burrow temperatures do not exceed lizard T_{set} even in the hottest part of the summer.

Climatic projections

In the RCP 4.5 scenario, our field site will have increased from its 23.5°C 2018 annual average to 24.5°C by 2079, and to 25.5°C at some point beyond 2099. For the RCP 8.5 scenario, our field site will have increased 1 to 24.5°C by 2059 and to 25.5°C by 2097. Assuming that equal warming occurs across

all microhabitats, the hours restricted to shade or burrows will not be impacted with a 1°C increase, but there will be an additional hour above T_{set} with a 2°C increase (Fig. 4). The number of hours restricted to burrows because T_b would exceed thermal variables will increase by 1–2 h. Currently, burrow temperatures do not exceed T_{pant} , VT_{max} or T_{set} , and a 1°C increase in temperatures will not change this. However, with a 2°C increase, burrows will exceed T_{set} for 1 h per day.

Discussion

In this study on the thermal ecology of *G. sila*, we have shown that these lizards exist in a very hot environment by taking refuge from extreme midday heat under *Ephedra* shrubs and inside *Dipodomys* burrows. Our analysis of monthly changes in lizard T_b reveals that daytime T_b does not significantly change over the course of their active season (Fig. 1a), indicating that despite mean monthly increases in ambient temperatures in this extremely hot environment, lizards are thermoregulating to keep their T_b consistent. This finding is consistent with other studies on diurnal lizards; for example, the skink *Tiliqua rugosa* thermoregulates at a relatively consistent $33\text{--}35^\circ\text{C}$ from spring through autumn by changing their thermoregulatory behaviours (Firth and Belan, 1998). In addition to shuttling among various microhabitats, thermoregulatory behaviours include changes in posture (Cowles and Bogert, 1944; Muth, 1977), lying flat on the ground when temperatures are low and raising limbs and tail off the ground when temperatures are high (Losos, 1987). In *G. sila*, night-time T_b was lower than daytime T_b and night-time T_b increased in July, most likely because the temperatures of the burrows they inhabit at night also increased. Over the course of the active season from May to July, lizards increased burrow use and decreased time spent in the open. At the beginning of the season, milder ambient temperatures allowed the lizards to stay above ground longer and utilized the open to defend territories, forage and mate (Buckley *et al.*, 2015; Grimm-Seyfarth *et al.*, 2017; Germano, 2019). As temperatures in each of these microhabitats increased, we observed an increased reliance on burrows and, to a lesser extent, shade plants when temperatures in the open are too high for these lizards to stay active for extended periods of time because they exceed the lizards' T_{set} and T_{pant} .

Analysis of the biophysical models we placed out in the three major microhabitats available to lizards at our field site during an extremely hot window of their active season in July revealed the following patterns relevant to lizard thermoregulatory behaviour: (i) temperatures in the open are highest during midday and lowest at night, with the greatest daily fluctuation, (ii) temperatures in burrows are the most stable, providing the lowest temperatures available during midday and the highest at night across all three microhabitats, and (iii) temperatures under shrubs tend to be intermediate between the open and burrows, suggesting that the shade from shrubs should provide a buffer from solar radiation to lizards during

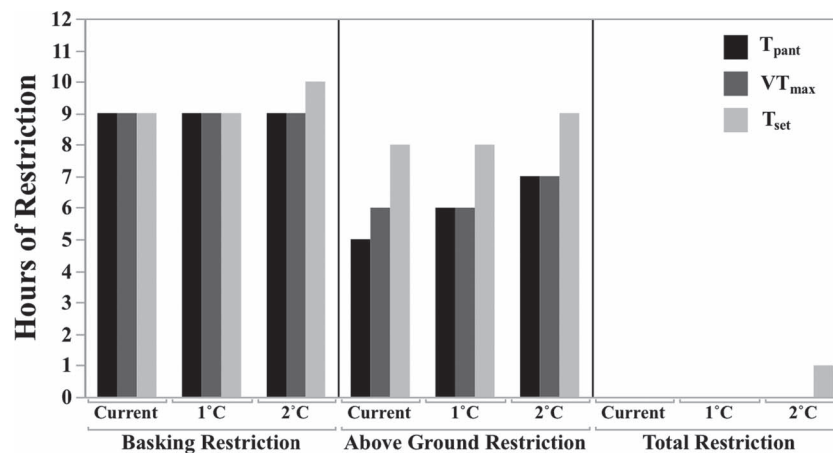


Figure 4: The number of daytime hours (0700 to 1900) that *Gambelia sila* are restricted from being in the open (basking restriction), from being in the open or shade (above ground restriction), or from being inside burrows (total restriction) calculated as hours above T_{pant} , VT_{max} and T_{set} , at the current climate and with 1 and 2°C increase in temperature. These data encompass a very hot portion of the active season (1–19 July), so there will be fewer restricted hours earlier in the season when daytime ambient temperatures are lower

midday. Lizard T_b was lowest in the early morning hours when inside burrows and increased rapidly upon emergence from burrows in the morning. In the morning, T_b is actually slightly elevated above T_e in the sun, which may be an artefact of the faster heating rates of the externally attached radio-transmitters than the biophysical models. However, this difference between lizard T_b and sun T_e is negligible until about 0900 h, when T_e in the sun dramatically exceeds lizard T_b . As a result of shuttling thermoregulatory behaviour, lizard T_b during the hottest part of the year tends to lie between that of the biophysical models in the shade of shrubs and those in burrows. Thermoregulation allowed lizards to maintain a fairly stable T_b during midday and to remain within their T_{set} for a small portion of the day. Lizard T_b tended to exceed T_{set} during the hours of 1400–1900, probably because lizards traded off their T_{set} with the need to be above ground to defend territory and forage (Martin and Lopez, 1999; Polo *et al.*, 2005; Medina *et al.*, 2016). It is fairly common for diurnal lizards to allow their T_b to exceed their lab-measured T_{set} (e.g. Light *et al.*, 1966), sometimes even panting in order to evaporatively cool while active in extreme heat (reviewed in Tattersall *et al.*, 2006). During the latter portion of the day, lizard T_b started to slowly decline as they entered burrows.

Collecting data on T_{set} and field active T_b allowed us to examine the lizards' thermoregulatory accuracy (d_b) during daylight hours, when they can actively thermoregulate. Early in the morning, d_b is low because all three microhabitats are too cold for the lizards to achieve their preferred body temperatures. Interestingly, average T_b in the early morning is actually higher than all three microhabitats (Fig. 2), which may be a result in part from solar radiation heating up the external radio-transmitter more rapidly than the biophysical models. In addition, lizards may be thermoregulating by positioning their bodies perpendicular to the sun to absorb more solar

radiation (Muth, 1977; Waldschmidt, 1980), standing on all four legs to avoid conductive heat loss to the ground (Cowles and Bogert, 1944), darkening their skin via melanophore dispersion to absorb more radiation (Sherbrooke *et al.*, 1994; Sherbrooke, 1997), and other mechanisms. Thermoregulatory accuracy is best at around 9 am, when lizard T_b matches their T_{set} . As the day progresses, d_b becomes worse as available temperatures are higher and therefore further from T_{set} . They shuttle between burrows (where there is good thermal quality but no opportunity to forage, defend territories, etc.) and the open desert floor (poor thermal quality but facilitates the above behaviours). During the heat of the day, lizards can either seek refuge in burrows or continue above-ground activity, at least for a time, by using *Ephedra* shrubs (Westphal *et al.*, 2018). Our data support the hypothesis that shrubs are valuable and aid in the thermoregulation of *G. sila* because on a hot day, they are currently able to spend four more hours above ground than if there were no shrubs and they were forced to enter burrows to avoid exceeding T_{pant} . Furthermore, light can penetrate shrub canopies, resulting in a mosaic of thermal and radiative properties, so the thermal microhabitat under shrubs may be even more complex and variable than our biophysical models could measure. All biophysical models under shrubs were placed on the ground; in hindsight, after we realized that lizards sometimes climbed several inches off the ground into shrubs, we realized that placing models on shrub branches would have been an informative way of analyzing microhabitat heterogeneity underneath shrubs, as lizards could thermoregulate more accurately during the heat of the day by climbing in shrubs (Germano, 2019). Shrubs may therefore provide a valuable source of thermal heterogeneity in this relatively simple environment, a pattern that has been observed in many other studies (Bauwens *et al.*, 1996; Bauwens *et al.*, 1999; Stout *et al.*, 2013; Sears *et al.*, 2016; Filazzola *et al.*, 2017). For example, Egyptian

tortoises (*Testudo kleinmanni*) in the deserts of Egypt depend on large shrubs to thermoregulate and survive; if loss of vegetation occurred, the species would not persist (Attum *et al.*, 2013). In general, thermal resources like shade may be important buffers for the effects of climate change, especially for organisms inhabiting areas experiencing rapid warming (Suggitt *et al.*, 2018). Given that *G. sila* do occur in sites without shrubs (Germano and Rathbun, 2016), we recommend future studies comparing the thermoregulatory accuracy and activity patterns of *G. sila* populations with and without shrubs would be informative.

Field-active lizards thermoregulate to achieve and maintain T_b within their T_{set} range, which is optimal for peak performance (e.g. sprint speed, reproduction, or digestion, Xiang *et al.*, 1996). While lizards by definition prefer to thermoregulate within their T_{set} range, they regularly exceed T_{set} to perform essential activities like feeding and mating (Porter *et al.*, 1973; Adolph and Porter, 1993; Bauwens *et al.*, 1996), so examining their VT_{max} in the field is ecologically relevant. Similarly, measures of upper thermal tolerance like the CT_{max} are important because lizards *cannot* exceed these temperatures because they would lose motor function and die (Cowles and Bogert, 1944). If habitats become hot enough that lizards will exceed their CT_{max} for significant portions of the day, extirpation is likely to occur because the lizards will lack sufficient activity time, as *G. sila* is already restricted from basking in the open or even being above ground at all for large portions of the day. Clearly, shuttling behaviour mitigates these restrictions; lizards can still move through hot, open areas in the middle of the day as long as they consistently seek refuge under shrubs or in burrows to cool off. However, the current hours of restriction (ranging from 5–10 h per day depending on the metric used, Fig. 4) are extremely high (Sinervo *et al.*, 2010), suggesting that these lizards may already be dramatically restricted by high temperatures. The number of restriction hours may be slightly overestimated because we used external radio-transmitters, which may read higher T_b than the actual internal T_b , especially when they are basking in the sun. However, lizards spend a small quantity of time in the sun during this hot time of year (Fig. 1b), so our overestimates are likely to be minor. The high number of restriction hours, along with factors like extreme aridity, might explain why *G. sila* enter aestivation and why they have such a short active season (Germano *et al.*, 1994). Clearly, *G. sila* is adapted to hot, arid environments, as evidenced by its ability to be active at high ambient temperatures (Germano, 2019), its high thermal tolerance and its persistence in desert ecosystems. However, how long will it be before ambient temperatures become high enough that lizards cannot physiologically and behaviourally mitigate them?

Unsurprisingly, anthropogenic climate change is likely to exacerbate the already hot climate in the San Joaquin Desert and impact *G. sila*. Our models predict that as temperatures increase, *G. sila* will continue to lose hours of activity because of microhabitat temperatures surpassing T_{pant} (and theoretic-

cally also their CT_{max}), VT_{max} and T_{set} . The restriction hours for T_{pant} and VT_{max} were similar because the temperatures for T_{pant} and VT_{max} were similar (Fig. 2, Camacho *et al.*, 2018). As global temperatures continue to rise, there will be a resulting shift in the distribution of local species populations and changes in timing of activity (Parmesan and Yohe, 2003; Root *et al.*, 2003; Sinervo *et al.*, 2017). However, at the rate of climate change occurring, lizards may not be capable of responding to increasing temperatures. On the one hand, having shade-providing shrubs in this heterogeneous habitat may aid in the resilience of this species to a rising climate (Germano, 2019). On the other hand, behavioural thermoregulation (for example, use of shrub shade) can actually *prevent* lizards from adapting to climate change because higher thermal tolerance is not being selected for (Huey *et al.*, 2003; Buckley *et al.*, 2015). Furthermore, the projected changes in biophysical models by 1 and 2°C ignore the spatial heterogeneity of the environment (Sears *et al.*, 2011), and actual changes could be very different because microhabitat temperatures will increase at different rates than ambient temperatures. Our data show that conditions inside burrows, which have the lowest temperatures during midday, will exceed the T_{set} of *G. sila* with a 2°C increase in temperatures by the end of the century. Notably, this relies on temperatures of biophysical models placed 1 m into a burrow, and it is possible that lizards could move deeper into burrow systems to maintain preferred temperatures. Future studies will examine depth and complexity of kangaroo rat burrow systems. If burrows cannot provide an adequate thermal buffer to lizards in the future, then lizards will experience an increase in energy expenditure throughout the day without the available time to forage. This additional energy expenditure in the face of climate change will exacerbate the potential for decreased energy for reproduction and growth (Sears *et al.*, 2011, Sinervo *et al.*, 2017). Clearly, evidence-based and proactive management of kangaroo rat burrows and shade-providing shrubs are essential to the persistence of *G. sila* in the Carrizo Plain in the future. If nothing is done to mitigate the effects of climate change and make important decisions about the management of this habitat, the extirpation of this population and potentially extinction of the entire species is a distinct possibility.

Funding

This research was generously supported by the William and Linda Frost Fund in the Cal Poly College of Science and Mathematics, by the Bureau of Land Management, the Nature Conservancy and the Cal Poly Biological Sciences Department.

Acknowledgements

We are grateful to B Axsom of BLM for logistical assistance and HS Butterfield of The Nature Conservancy for contribut-

ing to the purchase of radio-transmitters. We are also grateful to K Bodwin and A Marquardt for advice on statistical analysis. Thank you to J Hurl, B Blom and E Zaborsky who helped make this happen. We thank the following people for assistance with field work: A Bjerre, M Corn, D Deaser, N Duong, T Eldib, G Espinosa, G Garcia, E Gondwana, S Gonzales, JT Hussey, M Kepler, C Knowd, P Maier, F Macedo, H Neldner, T Nhu, JT Nolan, J Parker, K Rock, D Rypka, M Solis, T Stratton, S Van Middlesworth, R Seymour, A Valdivia and J Whelan.

References

- Adolph SC, Porter WP (1993) Temperature, activity, and lizard life histories. *Am Nat* 142: 273–295.
- Attum O, Kramer A, Baha El Din SM (2013) Thermal utility of desert vegetation for the Egyptian tortoise and its conservation implications. *J Arid Environ* 96: 73–79.
- Bashey F, Dunham AE (1997) Elevational variation in the thermal constraints on and microhabitat preferences of the greater earless lizard *Cophosaurus texanus*. *Copeia* 1997: 725–737.
- Bauwens D, Hertz PE, Castilla AM (1996) Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* 77(6):1818–1830.
- Bauwens D, Castilla AM, Mouton PFN (1999) Field body temperatures, activity levels and opportunities for thermoregulation in an extreme microhabitat specialist, the girdled lizard (*Cordylus macropholis*). *J Zool* 249: 11–18.
- Bradshaw SD, Main AR (1968) Behavioural attitudes and regulation of temperature in *Amphibolurus* lizards. *J Zool* 154: 193–221.
- Brattstrom BH (1965) Body temperatures of reptiles. *Am Midl Nat* 73: 376–422.
- Brusch GA IV, Taylor EN, Whitfield SM (2016) Turn up the heat: thermal tolerances of lizards at La Selva, Costa Rica. *Oecologia* 180: 325–334.
- Buckley LB, Ehrenberger JC, Angilletta MJ (2015) Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. *Func Ecol* 29: 1038–1047.
- California Energy Commission (2019) *Cal-Adapt: Exploring California's Climate Change Research*. State of California. <http://cal-adapt.org/> (last accessed 13 September 2019).
- Camacho A, Rusch T, Ray G, Telemeco R, Trefaut Rodriguez M, Angilletta MJ (2018) Measuring behavioral thermal tolerance to address hot topics in ecology, evolution, and conservation. *J Therm Biol* 73: 71–79.
- Carroll JM, Davis CA, Fuhlendorf SD, Elmore RD (2016) Landscape pattern is critical for the moderation of thermal extremes. *Ecosphere* 7: e01403. <https://doi.org/10.1002/ecs2.1403>.
- Cowles RB, Bogert CM (1944) A preliminary study of the thermal requirements of desert reptiles. *Bull Am Mus Nat Hist* 83: 265–296.
- D'Antonio CM, Malmstrom CM, Reynolds SA, Gerlach J (2007) Ecology of invasive non-native species in California grassland. In MR Stromberg, JD Corbin, CM D'Antonio, eds, *California Grasslands: Ecology and Management*. University of California Press, Berkeley, pp. 67–83.
- Dawson WR, Templeton JR (1963) Physiological responses to temperature in the lizard *Crotaphytus collaris*. *Physiol Zool* 36: 219–236.
- Działowski EM (2005) Use of operative temperature and standard operative temperature models in thermal biology. *J Therm Biol* 30: 317–334.
- Filazzola A, Westphal M, Powers M, Liczner AR, Smith Woollett DA, Johnson B, Lortie CJ (2017) Non-trophic interactions in deserts: facilitation, interference, and an endangered lizard species. *Basic Appl Ecol* 20: 51–61.
- Firth BT, Belan I (1998) Daily and seasonal rhythms in selected body temperatures in the Australian lizard *Tiliqua rugosa* (Scincidae): field and laboratory observations. *Physiol Zool* 71: 303–311.
- Germano DJ, Williams DF, Tordoff W III (1994) Effect of drought on blunt-nosed leopard lizards (*Gambelia sila*). *NW Nat* 75: 11–19.
- Germano DJ, Rathbun GB, Saslaw LR, Rathbun GB, Saslaw LR (2001) Managing exotic grasses and conserving declining species. *Wildl Soc Bull* 29: 551–559.
- Germano DJ, Williams DF (2005) Population ecology of blunt-nosed leopard lizards in high elevation foothill habitat. *J Herpetol* 39: 1–18.
- Germano DJ, Rathbun GB, Saslaw LR, Cypher BL, Cypher EA, Vredenburg LM (2011) The San Joaquin Desert of California: ecologically misunderstood and overlooked. *Nat Areas J* 31: 138–147.
- Germano DJ, Rathbun GB (2016) Home range and habitat use by blunt-nosed leopard lizards in the southern San Joaquin Desert of California. *J Herpetol* 50: 429–434.
- Germano DJ (2019) Activity and thermal biology of blunt-nosed leopard lizards (*Gambelia sila*) in the San Joaquin Desert of California. *West N Am Nat* 79: 428–440.
- Grant BW, Dunham AE (1988) Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* 69: 167–176.
- Grimm-Seyfarth A, Mihoub J-B, Henle K (2017) Too hot to die? The effects of vegetation shading on past, present, and future activity budgets of two diurnal skinks from arid Australia. *Ecol Evol* 7: 6803–6813.
- Gunderson AR, Stillman JH (2015) Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *P Roy Soc B-Biol Sci* 282: 20150401.
- Heatwole H, Firth BT, Webb GJW (1973) Panting thresholds of lizards—I. Some methodological and internal influences on the panting threshold of an agamid, *Amphibolurus muricatus*. *Comp Biochem Physiol A: Physiol* 46: 799–826.
- Hertz PE, Huey RB, Stevenson RD (1993) Evaluating Temperature Regulation by Field-Active Ectotherms: The Fallacy of the Inappropriate Question. *The American Naturalist* 142: 796–818.

- Huey RB, Hertz PE, Sinervo B (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am Nat* 161: 357–366.
- IUCN (2017) The IUCN Red List of Threatened Species. Version 2017.3. <https://www.iucnredlist.org/species/40690/10336468>. (last accessed 13 September 2019).
- JMP®, Version Pro 14. SAS Institute Inc., Cary, NC, 1989–2019.
- Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *PNAS* 106: 3835–3840.
- Larson MW (1961) The critical thermal maximum of the lizard *Sceloporus occidentalis occidentalis* Baird and Girard. *Herpetologica* 17: 113–122.
- Light P, Dawson WR, Shoemaker VH, Main AR (1966) Observations on the thermal relations of Western Australian lizards. *Copeia* 1966: 97–110.
- Lortie CJ, Filazzola A, Sotomayor DA (2015) Functional assessment of animal interactions with shrub-facilitation complexes: a formal synthesis and conceptual framework. *Func Ecol* 30: 41–51.
- Losos JB (1987) Postures of the military dragon (*Ctenophorus isolepis*) in relation to substrate temperature. *Amphibia-Reptilia* 8: 419–423.
- Martín J, López P (1999) When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behav Ecol* 10: 487–492.
- Medina M, Fernández JB, Charruau P, Méndez de la Cruz F, Ibarguen-goytia N (2016) Vulnerability to climate change of *Anolis allisoni* in the mangrove habitats of Banco Chinchorro Islands, Mexico. *J Therm Biol* 58: 8–14.
- Milling CR, Rachlow JL, Olsoy PJ, Chappell MA, Johnson TR, Forbey JS, Shipley LA, Thornton DH (2018) Habitat structure modifies microclimate: an approach for mapping fine-scale thermal refuge. *Methods Ecol Evol* 9: 1648–1657.
- Moore D, Stow A, Kearney MR (2018) Under the weather? The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system. *J Anim Ecol* 87: 660–671.
- Minnich RA (2008) *California's Fading Wildflowers: Lost Legacy and Biological Invasions*. University of California Press, Berkeley.
- Muth A (1977) Thermoregulatory postures and orientation to the sun: a mechanistic evaluation for the zebra-tailed lizard, *Callisaurus draconoides*. *Copeia* 1977: 710–720.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- Pike DA, Mitchell JC (2013) Burrow-dwelling ecosystem engineers provide thermal refugia throughout the landscape. *Anim Cons* 16: 694–703.
- Polo V, López P, Martín J (2005) Balancing the thermal costs and benefits of refuge use to cope with persistent attacks from predators: a model and an experiment with an alpine lizard. *Evol Ecol Res* 7: 23–35.
- Porter WP, Mitchell JW, Beckman WA, DeWitt CB (1973) Behavioral implications of mechanistic ecology: thermal and behavioral modeling of desert ectotherms and their microenvironment. *Oecologia* 13: 1–54.
- Powers RP, Jetz W (2019) Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat Clim Change* 9: 323–329.
- Prieto AA, Whitford WG (1971) Physiological responses to temperature in the horned lizards, *Phrynosoma cornutum* and *Phrynosoma douglassii*. *Copeia* 1971: 498–504.
- R Core Team (2017) R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. <https://www.R-project.org/> (last accessed 13 September 2019).
- Raws USA Climate Archive, Western Regional Climate Center, <https://raws.dri.edu/index.html> (last accessed 13 September 2019).
- Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.
- Schiffman PM (2007) Species composition at the time of first European settlement. In MR Stromberg, JD Corbin, CM D'Antonio, eds, *California Grasslands: Ecology and Management*. University of California Press, Berkeley, pp. 52–56.
- Sears MW, Raskin E, Angilletta MJ Jr (2011) The world is not flat: defining relevant thermal landscapes in the context of climate change. *Int Comp Biol* 51: 666–675.
- Sears MW, Angilletta MJ Jr, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW, Mitchell WA (2016) Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *PNAS* 113: 10595–10600.
- Shea TK, DuBois PM, Claunich NM, Murphey NE, Rucker KA, Brewster RA, Taylor EN (2016) Oxygen concentration affects upper thermal tolerance in a terrestrial vertebrate. *Comp Biochem Physiol A: Mol Int Physiol* 199: 87–94.
- Sherbrooke WC (1997) Physiological (rapid) change of color in horned lizards. *Amphibia-Reptilia* 18: 155–175.
- Sherbrooke WC, Castrucci d L, AM HME (1994) Temperature effects on in vitro skin darkening in the mountain spiny lizard, *Sceloporus jarrovi*: a thermoregulatory adaptation? *Physiol Zool* 67: 659–672.
- Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz M, Lara-Resendiz R, Martínez-Méndez N, Calderón-Espinosa ML et al. (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328: 894–899.
- Sinervo B, Reséndiz RAL, Miles DB, Lovich JE, Ennen JR, Cooper RD, Rosen PC, Stewart JAE, Santos JC, Jr JWS, et al. (2017) Climate change and collapsing thermal niches of Mexican endemic reptiles. *White Paper for the Environmental Working Group of the UC-Mexico Initiative*. <https://escholarship.org/uc/item/4xk077hp> (last accessed 13 September 2019).

- Souter NJ, Bull CM, Lethbridge MR, Hutchinson MN (2007) Habitat requirements of the endangered pygmy bluetongue lizard, *Tiliqua adelaidensis*. *Biol Cons* 135: 33–45.
- Stevenson RD (1985) The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *Am Nat* 126: 362–386.
- Stout D, Buck-Diaz J, Taylor S, Evens JM (2013) *Vegetation Mapping and Accuracy Assessment Report for Carrizo Plain National Monument*. California Native Plant Society. <https://www.cnps.org/wp-content/uploads/2018/04/carrizo-mapping-report-2013.pdf> (last accessed 13 September 2019).
- Suggitt AJ *et al.* (2018) Extinction risk from climate change is reduced by microclimatic buffering. *Nat Clim Change* 8: 713–717.
- Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *PNAS* 111: 5610–5615.
- Tattersall GJ, Cadena V, Skinner MC (2006) Respiratory cooling and thermoregulatory coupling in reptiles. *Resp Physiol Neurobiol* 154: 302–318.
- Thomas CD *et al.* (2004) Extinction risk from climate change. *Nature* 427: 145–148.
- Urban MC (2015) Accelerating extinction risk from climate change. *Science* 348: 571–573.
- U.S. Fish and Wildlife Service (1998) *Recovery Plan for Upland Species of the San Joaquin Valley*. U.S. Fish and Wildlife Service, California, pp. 1–319
- Waldschmidt S (1980) Orientation to the sun by the iguanid lizards *Uta stansburiana* and *Sceloporus undulatus*: hourly and monthly variations. *Copeia* 1980: 58–462.
- Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin J, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416: 389–395.
- Westphal MF, Noble T, Butterfield HS, Lortie CJ (2018) A test of desert shrub facilitation via radiotelemetric monitoring of a diurnal lizard. *Ecol Evol* 8: 12153–12162.
- Xiang J, Weiguo D, Pingyue S (1996) Body temperature, thermal tolerance and influence of temperature on sprint speed and food assimilation in adult grass lizards, *Takydromus septentrionalis*. *J Therm Biol* 21: 155–161.
- Zamora-Camacho FJ, Reguera S, Moreno-Rueda G (2016) Thermoregulation in the lizard *Psammodromus algirus* along a 2200-m elevational gradient in Sierra Nevada (Spain). *Int J Biometeorol* 60: 687–697.