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

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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; Bashey 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 (Bradhaw and Main, 1968; Souter et al., 2007; Pike and Mitchell, 2013; Lortie et al., 2015; Moore et al., 2018; Suggit 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 palpatated 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 lizard’s 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 ∼ 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 × 20 × 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 ±1°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 $T_b$ and +2°C $T_b$). 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).
temperatures consistently about 6–8°C higher than night-time temperatures increased from daytime to night-time ambient temperatures increased from May to June to July, as expected, with daytime average temperatures increased from daytime Tb of lizards was significantly higher than night-time that night-time Tb increased significantly in July compared to May and June, presumably because burrow temperatures increased. The calculated VT\textsubscript{max} of G. sila was 40.4±0.8°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 Tb of G. sila during an extremely hot part of their active season (1–19 July 2019) is shown in Fig. 2, along with T\textsubscript{set} range, T\textsubscript{pant} and T\textsubscript{e} in the three microhabitats (results below).

**Preferred body temperature (T\textsubscript{set}) and thermoregulatory accuracy (d\textsubscript{b})**

The median preferred body temperature of G. sila is 34.1±1.2°C, with a T\textsubscript{set} range of 32.3±1.2–37.5±1.1°C (Fig. 2). There was no significant effect of sex (F\textsubscript{1} = 3.93, P = 0.08), SVL (F\textsubscript{1} = 0.02, P = 0.90), mass (F\textsubscript{1} = 0.26, P = 0.62), capture method (F\textsubscript{1} = 0.55, P = 0.47) or time of day (F\textsubscript{4} = 1.10, P = 0.41) on T\textsubscript{set}. Before 9 am, d\textsubscript{b} values were negative because lizard Tb was lower than T\textsubscript{set}; as even burrows are too cool for lizards to achieve T\textsubscript{set} at night and early morning (Fig. 3). After about 1100, d\textsubscript{b} values become positive as lizard Tb often exceeded T\textsubscript{set}, especially from about 1400 to 1900 (see Fig. 3).

**Results**

**Field active body temperature (T\textsubscript{b}) and microhabitat use**

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

**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 nighttime ambient temperatures (T\textsubscript{amb}) increased as the season progressed, but lizard Tb remained constant during daytime hours as they thermoregulated. Night-time Tb 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.

**Figure 2:** Average daily temperatures of biophysical models in three microhabitats (N = 6 each) and Gambelia sila body (Tb) 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\textsubscript{pant}), whereas temperatures in burrows were most often within lizard preferred body temperature (T\textsubscript{set}) range. Average maximum voluntary body temperature (VT\textsubscript{max}) did not exceed T\textsubscript{pant}. Lizards maintained Tb within T\textsubscript{set} for most of the daylight hours, and lizard Tb never exceeded T\textsubscript{pant}. Error bars represent ±1 SEM.
Thermoregulating within the $T_{\text{set}}$ range. As values move away from zero in either direction, the accuracy of thermoregulation decreases.

**Upper thermal tolerance ($T_{\text{pant}}$)**

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 $T_{\text{pant}}$. Mean $T_{\text{pant}}$ was 41.4 ± 0.2°C (Fig. 2). Given that the true upper thermal threshold ($CT_{\text{max}}$) is usually several degrees higher than $T_{\text{pant}}$ (e.g. Heatwole et al., 1973; Shea et al., 2016), the $CT_{\text{max}}$ 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 ($F_{4,33} = 11.07, P < 0.0001$), 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 exceeded all three thermal variables ($T_{\text{pant}}$, $VT_{\text{max}}$ and $T_{\text{set}}$). Even the ground beneath shrubs is above $T_{\text{pant}}$ for 5 h a day, where lizards are restricted to using burrows only. Currently, mean burrow temperatures do not exceed lizard $T_{\text{set}}$ 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 $T_{\text{set}}$ 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 $T_{\text{pant}}$, $VT_{\text{max}}$ or $T_{\text{set}}$, and a 1°C increase in temperatures will not change this. However, with a 2°C increase, burrows will exceed $T_{\text{set}}$ 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 33–35°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’ $T_{\text{set}}$ and $T_{\text{pant}}$.

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...
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 shutting 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). Shrub 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).
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, shutting 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 theoretically 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 $T_{max}$ 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 burrow systems is 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.

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