Habitat heterogeneity affects the thermal ecology of an endangered lizard

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Funding information
Funding for this research was provided by the Bureau of Land Management, the William and Linda Frost Fund in the Cal Poly College of Science and Mathematics, and the Bridges to the Baccalaureate Program between Allan Hancock College and the California Polytechnic State University funded by the National Institute of Health.

Abstract
Global climate change is already contributing to the extirpation of numerous species worldwide, and sensitive species will continue to face challenges associated with rising temperatures throughout this century and beyond. It is especially important to evaluate the thermal ecology of endangered ectotherm species now so that mitigation measures can be taken as early as possible. A recent study of the thermal ecology of the federally endangered Blunt-nosed Leopard Lizard (Gambelia sila) suggested that they face major activity restrictions due to thermal constraints in their desert habitat, but that large shade-providing shrubs act as thermal buffers to allow them to maintain surface activity without overheating. We replicated this study and also included a population of G. sila with no access to large shrubs to facilitate comparison of the thermal ecology of G. sila populations in shrubless and shrubbed sites. We found that G. sila without access to shrubs spent more time sheltering inside rodent burrows than lizards with access to shrubs, especially during the hot summer months. Lizards from a shrubbed site had higher midday body temperatures and therefore poorer thermoregulatory accuracy than G. sila from a shrubless site, suggesting that greater surface activity may represent a thermoregulatory trade-off for G. sila. Lizards at both sites are currently constrained from using open, sunny microhabitats for much of the day during their short active seasons, and our projections suggest that climate change will exacerbate these restrictions and force G. sila to use rodent burrows for shelter even more than they do now, especially at sites without access to shrubs. The continued management of shrubs and of burrowing rodents at G. sila sites is therefore essential to the survival of this endangered species.

KEYWORDS
activity restriction, burrows, climate change, shade, shrubs, thermoregulation
1 INTRODUCTION

Many organisms are threatened by the projected increase in global temperatures. As ectotherms, reptiles are disproportionately threatened because their body temperatures are dependent on the temperatures of their environment (Aragón et al., 2010). Models estimate that nearly 40% of lizard populations may be extirpated by 2080 (Sinervo et al., 2010), and heliothermic (sun-basking) lizards occupying the hottest habitats on the planet could be at particularly high risk because temperatures are already so high. Field observations of microhabitat use paired with comparisons of animals’ field-active and preferred body temperatures to the available microhabitat temperatures can give insight into how an animal uses its thermal landscape (Burrow et al., 2001; Fawcett et al., 2019; Taylor et al., 2021). Such data can also be used to calculate the population’s hours of restriction, or the number of hours per day that temperatures in certain microhabitats exceed the animal’s preferred body temperature or their upper thermal tolerance and are therefore undesirable or unavailable for use. This information can be used to identify thermal and ecological parameters that may help conserve threatened reptiles and their communities. For example, shrubs and other vegetation are important contributors to the habitat heterogeneity that provides a mosaic of temperatures for effective thermoregulation by lizards (Basson et al., 2017; Goller et al., 2014), suggesting that shrubs may help buffer reptiles from climate change.

The Blunt-nosed Leopard Lizard (Gambelia sila) (Figure 1a) is an ectotherm that has been listed as federally endangered since 1967 because almost 90% of the species’ historical range has been converted into uninhabitable agricultural fields (U.S. Fish & Wildlife Service, 1998). Once ranging across the vast San Joaquin or California Central Valley, G. sila are now restricted to a few small patches of relatively undisturbed San Joaquin Desert habitat. These heliothermic lizards are adapted to the very hot and dry California San Joaquin Desert ecosystem, where already high temperatures are becoming even more extreme (Germano et al., 2011; Ivey et al., 2020). Adult G. sila are primarily only active for a quarter of the year (late April through mid-July) (Germano & Williams, 2005; Montanucci, 1965), during which time they experience high environmental temperatures (Ivey et al., 2020). They feed and breed in this short window, using Giant Kangaroo Rat (Dipodomys ingens) burrows for shelter at night and during the heat of the day (Prugh & Brashares, 2012), then entirely retreat into the burrows for most of the remaining nine months of the year. Lizards in many populations, but not all, associate with desert shrubs, including the large gymnosperm shrub Ephedra californica. Ephedra californica is a foundation species in the San Joaquin Desert community (Lortie et al., 2017) and facilitates the presence of community members, including G. sila (Filizzola et al., 2017; Lortie et al., 2017; Westphal et al., 2018), which select for shrubs at fine spatial scales (Germano & Rathbun, 2016).

Until recently, technological constraints have prevented researchers from collecting the continuous body temperature data necessary for studying the thermal ecology of a species such as G. sila. Advances in miniaturization and technology of radiotelemetry transmitters now allow for ample data collection on physiological aspects of small animals (Weaver et al., 2021). Ivey et al. (2020) studied the thermal ecology of G. sila at a single site with abundant shrubs in 2018 and found that shrubs appear to serve as an important thermal buffer from the heat of the sun, potentially allowing G. sila to remain aboveground instead of retreating underground where they would be unable to perform necessary daily activities (Ivey et al., 2020; Westphal et al., 2018). To further test this hypothesis, we studied G. sila in 2019 at the same site as Ivey et al. (2020), hereafter called Shrubbed, and added a second nearby site where G. sila had virtually no access to shrubs (Shrubless). This allowed us to further assess the importance of shrubs for thermoregulating G. sila that were experiencing otherwise similar environmental conditions, and therefore understand how important shrubs may be in ensuring this endangered species’ survival. If shrubs provide a thermoregulatory benefit to G. sila, then lizards with access to shrubs should be active aboveground longer and use rodent burrows less often during the day than lizards without access to shrubs. Additionally, lizards with access to shrubs should thermoregulate more accurately (i.e., field-active body temperatures closer to preferred body temperatures; Hertz et al., 1993) than lizards without access to shrubs, and should have fewer hours of restriction currently and in modeled future scenarios when ambient temperatures will rise. Identifying aspects of the environment, such as shrubs, that may help G. sila thermoregulate more efficiently is important for informing management efforts to protect this species and other sensitive San Joaquin Desert species from rising temperatures in some of the hottest, driest parts of the continent.

2 MATERIALS AND METHODS

2.1 Field sites and study species

A pair of sites, one dominated by E. californica and other smaller perennial shrubs (hereafter named Shrubbed), and the other with no E. californica and very few other shrubs (Shrubless), were selected on the Elkhorn Plain within the Carrizo Plain National Monument in California, USA (Figure 1b). Shrubless was selected because lizards had been seen in the area previously, and it was only 6.5 km away from Shrubbed where we have previously collected data. The sites are similar in size (400 m²), as well as climate and elevation. Microhabitat use and shrub association of lizards at Shrubbed were studied in 2016 (Westphal et al., 2018), and field-active body temperatures of lizards were regularly recorded there in 2018 (Ivey et al., 2020). Gambelia sila at Shrubbed had access to ample shade provided primarily by the aforementioned large E. californica shrubs. Shade was also available from smaller perennials such as Isocoma ocradenia and Gutierrezia californica and small annual plants such as Amsinckia sp. and nonnative grasses. In contrast, lizards at Shrubless had limited access to aboveground shade, which was provided by very few l. ocradenia, G. californica, and Astragalus sp. (mostly A. lentiginosus, sometimes A. oxyphysus), in addition to small annual forbs.
and grasses. Shrubless had only a few individual perennial shrubs in the entire site, and notably, these shrubs were only used by a total of two lizards whose territories happened to overlap with these shrubs. Therefore, the use of shrub-provided shade by lizards at Shrubless was extremely rare (see Results). Lizards at both sites had access to burrows, which were confirmed to be engineered by *D. ingens* from 5 nights of trapping with 61 traps at each site in August 2020. *Dipodomys ingens* were captured at both sites, with very small numbers of *D. nitratoides* at Shrubbed exclusively.

We captured twenty lizards at each site (*N* = 40 total) by hand-held lasso over the course of three days in late April 2019, and collected the following data for each lizard: sex, reproductive state in females (gravid or not), snout–vent length (SVL, ±0.5 mm), and mass (±1 g). Lizards were fitted with VHF temperature-sensitive radiotransmitter collars with 16 cm whip antenna (Holohil Model BD-2T Holohil Systems Ltd, Carp, Ontario, Canada, attached with epoxy to ball chain "collars") following the methods of Ivey et al. (2020), then released at their site of capture the same day. Throughout the season, several lizards lost their collars, and these collars were placed onto new lizards, such that a total of 47 individuals (22 Shrubbed, 25 Shrubless) were tracked from May through mid-July 2019 for an average of 53 ± 12 days. Those that lost collars likely represented predation events, although in some cases, collars could have slipped off. In addition to the lost collars that were recovered, four lizards and their collars disappeared (likely from being carried away by avian predators) or were lost deep in burrows (where the collar was excavated at the end of the season). Lizards with less than two weeks of valid temperature data were excluded from analyses. The final dataset included the following sample sizes: May—Shrubbed: *N* = 16, Shrubless: *N* = 17; June—Shrubbed: *N* = 16, Shrubless: *N* = 18; and July—Shrubbed: *N* = 16, Shrubless: *N* = 15.

2.2 | Microhabitat use

We tracked *G. sila* using a VHF receiver (R-1000 Telemetry Receiver, Communications Specialists, Inc., Orange, CA, USA) and 3-element Yagi antenna. Each lizard was tracked 1–2 times per day for six days per week over the course of their active season, from May through mid-July. The observations at both sites were evenly distributed among morning, midday, and afternoon, and the lizards were tracked in a random order to ensure that observations were spread out throughout the day. Each lizard’s microhabitat use was recorded as one of the following: in the shade of a plant (with plant species identified), in full sunlight, or underground in a burrow. A lizard was
designated as underground in a burrow if they were not visible from the burrow mouth; sometimes, lizards sat close to the entrances of burrows, but this was categorized as the open because most of their body, notably the temperature-sensitive radio collar, was in sunlight. We then calculated the percent of time *G. sila* used each microhabitat in May, June, and July at each site. To compare the probability that a lizard would be found underground (in burrows) between the two sites, we ran a mixed-effects logistic regression model in R (R Core Team, 2020; RStudio, 2020, lme4 package v. 1.1-26, Bates et al., 2015) with time as a polynomial, site and month as fixed effects, and lizard ID as a random effect.

At the end of the active season, we collected data on *D. ingens* burrow densities at each site by counting the number of active or recently inactive burrows (Bean et al., 2012) within 10 m along four 100-m randomly placed transects at each site. We compared the burrow densities at the Shrubbed and Shrubless sites with Welch’s *t*-test in R. We also collected data on perennial shrub densities by counting the number of perennial shrubs in a 10-m radius around 16 random points (Zuliani et al., 2021) at each site, and compared the densities with Welch’s *t*-test in R.

### 2.3 Temperature variables

At the center of each site, we installed a stationary 3-m tall solar-powered (Tycon RemotePro 2.5 W Solar Power system with Vikram Solar Eldora 10P solar panel) omni-antenna (Telonics Model RA-6B) and receiver with data acquisition system (Telonics TR-5 Option 320). We estimated the range for continuous, gap-free data collection with this antenna to be approximately 300 m. About every five minutes, the receiver logged the interpulse interval of the signal from each radio collar in range, and we downloaded these data from the receivers each week. Because the radiotransmitters were externally attached to the lizards, *T*~b~ values may represent an overestimation of core *T*~b~ because they can heat rapidly from solar radiation; however, surgical implantation of radiotransmitters is not possible in an endangered species such as *G. sila*. We used manufacturer-provided calibration curves and the program Vinny Graphics v2.07 to convert the interpulse intervals to field-active body surface temperatures, which act as estimates of lizard body temperature (*T*~b~). Prior to analysis, we removed any outliers greater than two standard deviations away from each lizard’s mean *T*~b~, as these likely represented glitches in the data acquisition system; such outliers were uncommon (<5% of data points).

To collect data on the environmental temperatures of the three available microhabitats to these lizards for the entirety of the study, we deployed lizard physical models in sunlight, in the shade, and inside burrows, using the same models as Ivey et al. (2020). Models consisted of copper pipes (2.5 cm diameter and 12 cm long) capped with PVC and spray-painted matte gray and matte tan to resemble the color of the lizards’ skin. Models that were placed under shrubs and in the open were given two “legs” in the form of metal wire looped around the pipes so they could be propped up to resemble *G. sila* resting posture. Each model housed a Thermochron iButton (DS1921G-F5) programmed to record temperature every hour, on the hour. While empty models provide instantaneous operative temperature, we chose to fill the models with water to mimic a body cavity (Dzialowski, 2005) and to replicate the exact methods of Ivey et al. (2020); we also added plumber’s tape before screwing on the caps to maintain watertight seals. We placed the models haphazardly at each site (Shrubbed: *N* = 4 under *E. californica* shrubs, *N* = 4 in the open, and *N* = 4 anchored about 0.5 m inside the mouths of burrows; Shrubless: *N* = 4 in the open and *N* = 4 anchored inside the mouths of burrows). Models inside *D. ingens* burrows and under shrubs received little to no solar radiation, whereas models in the open were exposed to full sunlight during daylight hours. The models under shrubs and in the open were placed facing north, south, east, and west, and the orientations of the burrow mouths were recorded. Every two weeks, we downloaded the iButton data using OneWireViewer (Maxim Integrated), refilled the models with water, and returned them to the same locations. Physical model temperatures in the three microhabitats were treated as operative temperatures (*T*~b~) in analyses (see below), where *T*~b~ represents the effective microhabitat temperatures available to *G. sila*.

### 2.4 Preferred body temperature and thermoregulatory accuracy

As *G. sila* aestivation approached in mid-July, we recaptured and reprocessed each lizard and removed their collars. Before returning each lizard to its capture site, we collected data on its preferred body temperature (*T*~set~) in a thermal gradient as described in Ivey et al. (2020). The gradient consisted of 3 lanes (250 × 20 × 25 cm) filled with sand substrate and separated by wood dividers, ranging from 47°C at the hot end to 10°C at the cool end. Three *G. sila* were placed into the center of the gradient at a time, each in its own lane, with thermocouples (Model 55RTC-TT-K-40-72; Omega Engineering, UK) in their cloacae recording body temperature every 10 min for three hours. These data were recorded on a data logger (Model RXDL4SD; Omega Engineering, Egham, Surrey, UK), and only the last hour of data was used for analysis.

We calculated average *T*~b~ for each of the two populations after removing outliers greater than 2 standard deviations away from each lizard’s mean, and we used the interquartile range (IQR) of each population as its *T*~b~ range. Since there was no significant difference in *T*~b~ between the two populations (see Results), we used the mean *T*~b~ IQR of all lizards for the following analyses. We calculated lizard thermoregulatory accuracy (*d*~b~) by subtracting the mean *T*~b~ IQR from each instance of *T*~b~ in the field (Hertz et al., 1993). When *T*~b~ fell within *T*~set~ IQR, *d*~b~ was zero. Either very high positive or very low negative values of *d*~b~ represented poor thermoregulatory accuracy because the field-active *T*~b~ was higher or lower than *T*~set~ range. Lizard *T*~b~ was also compared with the panting threshold (*T*~p~) of *G. sila*, a measure of upper thermal tolerance that Ivey et al. (2020) measured.
in 2018. All $d_b$ values for each lizard were averaged by hour per day from 0.700 to 2.000 (daylight hours when lizards can actively thermoregulate), then each hour’s $d_b$ values were averaged to create hourly $d_b$ values per month. To compare the thermoregulatory accuracy of G. sila at Shrubbed and Shrubless, $d_b$ values were further averaged to give one value per lizard per month. We then performed a multifactor ANOVA with $d_b$ as the response variable; site, month, and the site x month interaction as fixed factors; and lizard ID as a random factor nested within site, using JMP (SAS Institute Inc., v. 14.3. 2018).

2.5 | Hours of restriction and climatic projections

We compared temperatures from the physical models (T_d) to G. sila $T_{set}$ and $T_{pant}$ each hour of the day for each month to calculate the number of hours in a day that a given microhabitat would be thermally stressful (i.e., exceed either $T_{set}$ or $T_{pant}$) for a lizard. We designated hours of restriction as “basking restriction” when temperatures in open sunlight were too hot and lizards therefore must remain in shade or in burrows; “aboveground restriction” when temperatures in the open and shade of large shrubs were too hot and lizards therefore must retreat to burrows (this is only applicable for lizards at Shrubbed); and “total restriction” when all three microhabitats including burrows were too hot (Ivey et al., 2020).

Each of these hours of restriction variables was then recalculated by adding 1°C and 2°C to the $T_e$ values for each microhabitat, following the methods of Ivey et al. (2020) which used the Cal-Adapt representative concentration pathway (RCP) climate scenarios 4.5 and 8.5 to determine that 1-2°C represent likely mean temperature increases this century in the Elkhorn Plain (California Energy Commission, 2019).

3 | RESULTS

3.1 | Microhabitat use

From May through mid-July 2019, we collected 1.148 individual radiotelemetry observations of G. sila at Shrubbed and 1.019 observations of lizards at Shrubless. Shrub density was significantly different between the two sites (Shrubbed: 15.69 ± 4.02 shrubs/987 m², Shrubless: 0.56 ± 0.22 shrubs/987 m²; $t = 3.76$, $p = .002$). In May, lizards at both sites spent the majority of daytime hours basking in the open (Figure 2a). In June and July, lizards at both sites spent progressively less time in the open and more time in the shade of plants and in burrows than they did in May. Although some lizards at Shrubless found some shade from sparse annual plants and shrubs, they collectively spent very little time in the shade throughout the active season because shade was largely unavailable. In June and July, lizards from Shrubless spent 46% and 57% of their observed time, respectively, inside burrows, compared with 31% and 43% for lizards at Shrubbed. The probability that lizards at Shrubless would be found underground in D. ingens burrows instead of aboveground was higher than that for lizards at Shrubbed ($z = 4.35$, $p < .001$) throughout the season. Burrow density was not significantly different between the two sites (Shrubbed: 35.83 ± 4.71 burrows/100 m, Shrubless: 44.67 ± 6.26 burrows/100 m; $t = -1.36$, $p = .23$). Lizards at both sites most likely spent all their time in burrows at night.

The woody perennial shrubs most commonly used for shade by lizards at Shrubbed were G. californica, followed by I. acradenia, E. californica, and unidentifiable dead small shrubs, which were likely either I. acradenia or G. californica. One individual had access to and used E. fasciculatum (Figure 2b). In May, when annuals were plentiful, lizards at Shrubbed used the shade of Amsinckia sp. 52% of the time they were in shade, and this decreased to 19% and 10% in June and July, respectively, when lizards started using woody shrubs more often for shade (Figure 2b). Lizards at both sites also used annual or perennial Astragalus sp., as well as the annual forb E. gracillimum and nonnative grasses (primarily Schismus sp. and Bromus sp.) for shade.

3.2 | Thermoregulation

The mean $T_{set}$ for G. sila at Shrubbed was 34.1°C with IQR of 32.3–36.8°C, and mean $T_{set}$ for lizards at Shrubless was 35.0°C with IQR of 35.1–38.5°C. Because these values were not significantly different from one another ($t = -0.89$, $p = .38$), they were pooled to create a single $T_{set}$ IQR of 33.2–37.9°C for the G. sila in this study. This IQR is very similar to the IQR of 32.3–37.5°C used by Ivey et al. (2020).

Gambelia sila maintained $T_b$ within their $T_{set}$ during daylight hours in the month of May, but in June and July, their $T_b$ slightly exceeded $T_{set}$ for a majority of their active daytime hours (Figure 3), resulting in good $d_b$ in May and poorer $d_b$ in the hotter months of June and July (Figure 4). The mean $T_b$ of G. sila at each site never exceeded $T_{pant}$, although in June and July, the $T_e$ in open sunlight exceeded $T_{pant}$ for several hours, while the shrub and burrow $T_b$ stayed below $T_{pant}$ (Figure 3). $T_b$ of lizards at Shrubless was slightly lower than at Shrubbed but not significantly so (site: $F = 2.74$, $df = 1$, $p = .10$; month: $F = 243.15$, $df = 2$, $p < .0001$; site-by-month interaction: $F = 0.27$, $df = 2$, $p = .76$; Figure 3). As a day progressed, lizards moved from burrows to the open and then retreated under vegetation or back into burrows typically in the late afternoon when temperatures were highest (Figure 3). On average, lizards at Shrubbed thermoregulated more accurately than lizards at Shrubbed (site: $F = 77.39$, $df = 1$, $p < .0001$; month: $F = 193.71$, $df = 2$, $p < .0001$; site-by-month interaction: $F = 0.12$, $df = 2$, $p = .89$; Figure 4). In May, lizards at both sites thermoregulated fairly accurately ($d_b$ near 0 in the middle of the day), but lizards at Shrubbed thermoregulated more accurately than lizards at Shrubless (Figure 4). In June and July, G. sila at Shrubbed thermoregulated more accurately than lizards at Shrubbed. During these hot months, $d_b$ of lizards at Shrubbed was better in the
mornings and evenings but poorer during the day, whereas lizards at Shrubless kept their \( d_e \) closer to 0 during the day by staying in burrows more often than lizards at Shrubbed.

### 3.3 Hours of restriction and climatic projections

Because May temperatures are so mild, \( G. \) \textit{silis} do not currently experience any hours of restriction from using various microhabitats during daylight hours in May (Figure 5). However, in June and July, \( G. \) \textit{silis} are restricted from basking in sunlight (basking restriction) for \( 8-11 \) daylight hours because \( T_e \) exceeds \( T_{set} \) or for \( 6-8 \) daylight hours because \( T_e \) exceeds \( T_{part} \) (Figure 5). In June and July, \( G. \) \textit{silis} at Shrubbed experience one more hour of basking restriction than lizards at Shrubless (Figure 5). Lizards at Shrubbed are completely restricted from being aboveground (aboveground restriction) for \( 3 \) of the \( 12 \) hr in June and for \( 8 \) hr in July because \( T_e \) exceeds \( T_{set} \). Currently, \( T_e \) inside burrows at both sites never exceeds \( T_{set} \) or \( T_{part} \), and \( T_e \) under shrubs at Shrubbed never exceeds \( T_{part} \).

As expected, adding \( 1^\circ C \) and \( 2^\circ C \) to the \( T_e \) data resulted in additional projected hours of restriction associated with climate change for both populations in June and July (Figure 5). Lizards at Shrubbed will be restricted from basking in sunlight and thus staying within their \( T_{set} \) range for \( 9-10 \) daylight hours, and lizards at Shrubless will be similarly restricted for \( 8-11 \) hr. Notably, lizards at Shrubbed should still be able to stay aboveground for several hours under future climate change scenarios because of their access to the shade of a shrub, while lizards at Shrubless do not have this option. Even

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**FIGURE 2** Microhabitat use of \( G. \) \textit{silis} at Shrubbed and Shrubless over the course of their 3-month primary active season in 2019, showing (a) percent of time spent in the open sun, in the shade of annual and perennial plants, and in rodent burrows, and (b) use of plant species for shade at each site. Lizards at Shrubless spent more time inside burrows and less time in the shade of plants, and the plants they used were often annuals because woody shrubs were extremely rare at that site.
FIGURE 3  (a) Field-active body temperatures of *Gambelia sila* at a Shrubbed site and a Shrubless site in May, June, and July 2019, with gray shading representing 1 SEM; operative temperatures of three microhabitats (open sunlight, shade of plants, and rodent burrows); the dark lines represent means, the tan bar represents the lizard $T_{set}$ range as measured in a thermal gradient; and the dotted line is the panting threshold of *G. sila* (from Ivey et al., 2020). (b) The percent of observations in which lizards used each of the three microhabitats at each site for each month during daylight hours.
under conditions positing 1°C or 2°C increases in all microhabitats, temperatures in burrows should remain low enough for lizards to stay below their $T_{set}$.

4 | DISCUSSION

As predicted, we found that $G. sila$ that had access to shrubs spent more time aboveground than those that did not, as lizards at Shrubless spent more time inside $D. ingens$ burrows. However, unexpectedly, the presence of shrubs did not give $G. sila$ higher thermoregulatory accuracy. This was mainly because staying inside burrows for longer periods of time actually allowed lizards to remain closer to their preferred body temperature, suggesting a trade-off between thermoregulation and activity aboveground. There was no difference in $D. ingens$ burrow density between the two sites, indicating that the higher frequency of burrow use by $G. sila$ at Shrubless was not the result of more available burrows. Instead, lizards at Shrubless likely have to limit their time spent aboveground because they would become too hot in the open sunlight, while lizards at Shrubbed can retreat to the shade of a shrub when the open microhabitat becomes too hot.

Like Ivey et al. (2020), we found that $G. sila$ will be further constrained from being active aboveground under future climate change scenarios, with temperatures undesirable (above preferred) or unlivable (above thermal maximum) for many hours per day. This constraint, however, is mitigated by shrubs, as lizards with access to shrubs could remain aboveground for several hours longer than lizards with no such access. Taken together, our study shows that shrubs are important in buffering $G. sila$ from the effects of high temperatures, but $D. ingens$ burrows remain the most essential refugia from high temperatures both now and in the future.

4.1 | Microhabitat use—activity aboveground

The presence of shrubs allowed $G. sila$ to spend more time aboveground, potentially enabling them to continue patrolling for mates, looking for prey, or engaging in other activities. Although it is unknown whether $G. sila$ can hunt and/or mate underground, typically
FIGURE 5  Hours of restriction from using specific microhabitats for *Gambelia sila* at a Shrubbed Site and a Shrubless Site over the course of their 3-month primary active season in 2019, calculated as the number of daylight hours in which microhabitat operative temperature $T_e$ exceeds $T_{set}$ (orange) or $T_{pant}$ (green). Current data show estimates from 2019, and +1°C and +2°C data model increases in temperature due to climate change. In general, lizards at Shrubbed experienced about one more hour of restriction than lizards at Shrubless.
heliothermic, diurnal lizards conduct the majority of these behaviors aboveground. A critically endangered lizard in Australia, the Pygmy blue-tongue lizard (*Tiliqua adelaidensis*) spends the majority of its time underground inside burrows but still needs to exit its burrow to feed (Milne et al., 2003). This lizard has likely evaded extinction thus far due to the tolerable temperatures inside burrows, and artificially added burrows have increased their density (Souter et al., 2004). Burrows constitute crucial thermal refugia for other lizard species inhabiting hot, arid regions worldwide, and their importance is even more critical as temperatures rise (Fenner & Souter, 2004). Burrows play a critical role in allowing G. sila to hunt, find, and court mates, and defend territories, especially as temperatures in the open continue to rise. In our study, we did not examine whether there were consequences for the lizards spending less time aboveground at Shrubless in terms of hunting success or fitness. Such a study would further elucidate the importance of shrubs in allowing aboveground activity in G. sila.

### 4.2 Microhabitat use—shade

As the season progressed and the temperatures rose, the importance of shade increased for G. sila at both sites (Figure 2a). Lizards mostly used annuals early in the season when annual cover was thick and then used perennials more often as time went on (Figure 2b). Dense grasses reduce locomotion speed in lizards (Newbold, 2005), and G. sila prefer open ground (Warrick et al., 1998) and tend to avoid areas with invasive annual grasses (Filazzola et al., 2017; Germano et al., 2001; Hacking et al., 2013). However, our study shows that when shrubs are not available, G. sila can use annuals for shade. We did not place models underneath annuals to assess the thermal quality of this microhabitat, an excellent topic for future study. Although many ectotherms avoid areas with invasive grasses, the microhabitats under these grasses may actually be cooler than an undisturbed area and may theoretically provide a better thermal environment as temperatures rise (García & Clusella-Trullas, 2019). In addition, we observed G. sila climbing annuals including grasses, especially at Shrubless, which could be a way to escape high surface temperatures or to gain a better view of the surroundings. *Astragalus* sp. were used much more often as shade by lizards at Shrubless than those at Shrubbed (Figure 2b) even though there were abundant *Astragalus* sp. at both sites. This may be because *Astragalus* sp. was the most abundant plant available for shade for lizards at Shrubless, which otherwise had only very sparse *I. acradenia* and *E. californica* and no *E. californica*. Surprisingly, *E. californica* was not the predominant shrub used by G. sila at Shrubbed in our study, which used *I. acradenia* and *G. californica* more often.

Numerous studies at Shrubbed in previous years documented more extensive use of *E. californica* by G. sila (Ivey et al., 2020; Lortie et al., 2020; Westphal et al., 2018). Westphal et al. (2018) showed that G. sila select for large shrubs such as *E. californica* more than what would be expected based on shrub density, and Filazzola et al. (2017) showed that G. sila scat is found more frequently under *E. californica* canopies than in the open. Our study followed a relatively wet winter, and the smaller *I. acradenia* and *G. californica* shrubs may not have been as present during the studies conducted in previous years. The understories of *E. californica* were also smothered with tall nonnative grasses capitalizing on the shade provided by the shrub, which likely prevented G. sila from using them for shade as often as in previous years (Filazzola et al., 2017; Ivey et al., 2020; Westphal et al., 2018). This observation suggests that G. sila are flexible and can use shade from any plant, not just *E. californica*, which is important information for habitat management and restoration efforts.

Qualitatively, from our telemetry observations, the G. sila at Shrubbed seemed to use smaller perennial shrubs such as *I. acradenia* and *G. californica* more often than *E. californica* for thermoregulatory purposes, and instead seemed more likely to retreat to *E. californica* if they felt threatened. Large, dense shrubs provide lower temperatures than small shrubs (Kerr et al., 2008), but G. sila appear to use burrows when temperatures become really high. *Gambelia sila* may prefer to use smaller shrubs, when available, for thermoregulatory purposes because they provide cover from solar radiation with less obstruction of surrounding views, allowing these visually oriented lizards to better see prey, predators, mates, and rivals.

### 4.3 Thermoregulation

Thermoregulatory accuracy was higher for lizards at Shrubless than at Shrubbed, which was unexpected because we predicted that the ability to utilize shrubs would improve the thermoregulatory accuracy of G. sila. However, our result is consistent with the observation that $T_s$ in the open was higher at Shrubbed than at Shrubless (Figure 3), even though we chose these nearby sites as “matched” sites. Models inside burrows also warmed up faster in the morning at Shrubbed than at Shrubless in May, but not in June or July (Figure 3). The temperature variation between sites may reflect soil composition, reflectance, or other variables (Limb et al., 2008). Our results suggest that very small differences in environmental temperatures can impact body temperature and thermoregulatory accuracy in heliothermic lizards, and emphasize the importance of understanding the thermal landscape of a given environment (Milling et al., 2018), which has been shown via models to impact thermoregulation (Sears et al., 2016).
Another contribution to the better thermoregulatory accuracy of *G. sila* at Shrubless is that they spent more time in burrows during the middle of the day (Figure 2), where *T_e* is closer to *T_set*, while lizards at Shrubbed spent more time aboveground, both in open sunlight and in the extensive shade that is unavailable at Shrubless. It is possible that lizards at Shrubbed were able to risk operating at *T_e* higher than their *T_set* during the day because they have an available aboveground buffer in the form of ample shade, while lizards at Shrubless have to limit their time spent aboveground because they cannot risk becoming too hot before retreating into a burrow. Simulated models indicate that lizards are expected to conserve energy by thermoconforming in more homogeneous landscapes such as Shrubless (Basson et al., 2017); the lizards at Shrubless indeed spent less time in sunlight and therefore were more thermoconforming than lizards at Shrubbed. Notably, our *T_set* values may underestimate the true *T_set* of *G. sila*, given that we could only measure *T_set* for three hours and could not afford time to allow lizards extensive acclimation inside the gradient.

### 4.4 Predation risk and other site differences

The lack of shrubs at Shrubless may have consequences that extend beyond thermoregulation. More *G. sila* at Shrubless (*N = 6*) were lost to probable predation than at Shrubbed (*N = 1*). Indeed, there were more confirmed mortalities (dead lizard found with col- lar) at Shrubless (*N = 4*) than at Shrubbed (*N = 1*); some of these lizards had missing limbs, but otherwise, their bodies were mostly intact. Lost collars were likely lizards that were carried away by birds, which are common predators of *G. sila* (Germano, 2019). In addition, two collars at Shrubless were found with lizard entrails, suggesting that those lizards were killed by avian predators (Germano, 2019; Nelson, 1934). While sample sizes of dead and lost *G. sila* are too small to draw definitive conclusions, these data suggest that lizards at Shrubless might experience higher predation pressure than those at Shrubbed. Lack of large shrubs such as *E. californica* may allow birds of prey or other visually oriented predators such as snakes to more easily see and capture lizards on the desert floor. Predation may therefore be an additional reason why *G. sila* at Shrubless spent more time underground in rodent burrows than those at Shrubbed. Predator avoidance was found to be an even higher priority for lizards in choosing a microhabitat than thermoregulation in Velvet geckos (*Oedura lesueurii*, Downes & Shine, 1998), and Mediterranean lizards (*Psammodromus algirus*) avoided leafless shrubs in early spring because they could not hide from predators as easily (Martín & López, 1998). In accordance with this idea, *G. sila* were observed using *E. californica* for predator avoidance in our study and in others (Filazzola et al., 2017; Montanucci, 1965; Westphal et al., 2018).

There are many other factors that may contribute to differences in activity and thermoregulation between lizards at our two sites, which we did not explicitly measure for this study. Abundance and composition of small arthropods that serve as the lizards’ prey (Germano et al., 2007) may be different between the two sites, especially since the vegetation composition is so different. There is also the possibility that soil composition is different between the two sites; anecdotal, the soil at Shrubbed is rockier than at Shrubless. This may have contributed to thermal differences on the ground that impacted lizard thermoregulation.

### 4.5 Hours of restriction and climatic projections

Our analysis of hours of restriction confirms the conclusion of Ivey et al. (2020) that *G. sila* are already thermally stressed, in that high temperatures force them to spend many hours in shade or inside burrows. Hours of restriction based on *T_b* were about 1 hr fewer on average compared with Ivey et al. (2020), and this is likely because their 2018 field season, and therefore their *T_b* used for analysis, occurred during a warmer summer than in 2019. With the anticipated increases of 1 or 2°C due to climate change, *G. sila* will likely face additional restriction during their active season. While lizards at both sites have relatively similar projected hours of restriction, lizards at Shrubbed will have on average one more hour of basking restriction than lizards at Shrubless. These data present an interesting conundrum: *G. sila* at Shrubless do not have aboveground shelter from the sun and from predators and therefore must spend more time inside burrows, but the slightly cooler temperatures on the open desert floor at Shrubless suggest that lizards there may actually experience fewer hours of restriction from basking in sunlight than lizards at the hotter Shrubbed site. However, lizards at Shrubbed still have the option of staying above-ground for more hours of the day than lizards at Shrubless because they can retreat to the cooler shade of shrubs.

Further increases in the number of hours of basking restriction or aboveground restriction are problematic because these lizards already are only active for about three months a year. Their ability to compensate for climate change by becoming active earlier in the year is limited because their activity would be stymied by the dense invasive annual vegetation that appears in February–March and only begins to be clipped by *D. ingens* and/or grazed by cattle in May as these lizards emerge from aestivation. Fortunately, our data suggest that *G. sila* are unlikely to be restricted from all their microhabitats even after a 2°C increase. Also, our projections merely added 1–2°C to current *T_e*, whereas certain microhabitats might actually warm at a slower rate, providing thermal buffers (Baust, 1976; González-del-Pliego et al., 2020; Scheffers, Brunner, et al., 2014; Scheffers et al., 2014). A more robust prediction would take into account these differences in warming rate for each microhabitat compared with ambient temperature, which would likely be more favorable for the lizards. Furthermore, we measured burrow *T_e* relatively close to the entrances of *D. ingens* burrows, and it is likely that temperatures are lower deeper inside these complex burrow networks. The fact that lizard *T_e* was lower than burrow *T_e* at night in May (Figure 3) supports this notion. As the climate warms, lizards may be able to move deeper inside these burrows to continue thermoregulating within their *T_set*. 
5 | CONCLUSION

We found that G. sila without access to shrubs are not necessarily in greater danger of overheating or losing hours of activity, as lizards at Shrubless thermoregulated closer to their $T_{set}$ than lizards from Shrubbed. While shrubs may play an important role in lizard thermoregulation, lizards at Shrubless spent more time in burrows and thermoregulated more accurately, suggesting that burrows are as important to the thermal ecology of G. sila as shrubs, or likely even more important. There also appears to be a trade-off between more accurate thermoregulation and activity spent aboveground, as implied by the fact that lizards at Shrubless had higher thermoregulatory accuracy and spent more time in burrows. In addition to deploying artificial shade structures (Ghazian et al., 2020), ensuring the continued presence of D. ingens may be essential in securing G. sila persistence. Burrows excavated by ecosystem engineers such as D. ingens are often critical to the survival of other community members (Pike & Mitchell, 2013; Prugh & Brashares, 2012).

Additionally, our data suggest that shrubs could be important in protecting G. sila from avian predators such as ravens, further underscoring the conclusion that the ideal habitat for G. sila is San Joaquin Desert with D. ingens precincts and shrubs. To ensure that our results are relevant to the conservation of G. sila across California’s San Joaquin Desert, expanding our methods to include additional populations of G. sila would provide a management-applicable understanding of how these lizards interact with their thermal landscape on multiple spatial scales (Steen, 2010). Recognizing the importance of water availability, another environmental factor that is becoming more and more limited in the San Joaquin Desert as droughts become more regular will also help us understand constraints faced by G. sila and other desert lizards that are facing similar stressors.

ACKNOWLEDGMENTS

We thank B Axsom, J. Hurl, and B Lindquist of BLM for logistical assistance, K Ivey for leading an original study on which this study was based, and the following people for their support: K Bodwin, D Brewster, R Brewster, M Corn, M Cornwall, J Cruz, K Doctor, N Duong, N Ghazian, K Glynn, E Gruber, P Hatch, JT Hussey, M Kepler, K Knowd, N Luong, F Macedo, K Meeder, H Neldner, T Nhu, JT Nolan, J Parker, K Paulsen, A Phelan-Roberts, J Raby, L Rivas, K Rock, M Rottenborn, R Seymour, M Solis, C Stenger, R Telemecc, C Thao, A Underwood, O Valencia-Soto, S Van Middlesworth, J Walker, A Waters, J Whelan, and M Zuliani. We acknowledge that the land on which our research was done carries the heritage and culture of the indigenous Northern Chumash and Yokuts tribes.

CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

Nicole Gaudenti: Conceptualization (supporting); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (equal); resources (supporting); software (equal); supervision (equal); validation (lead); visualization (lead); writing-original draft (lead); writing-review & editing (equal). Emmeleia Nix: Data curation (equal); writing-review & editing (supporting). Paul Maier: Data curation (lead); writing-review & editing (supporting). Michael F. Westphal: Conceptualization (equal); funding acquisition (lead); methodology (supporting); project administration (supporting); resources (lead); writing-review & editing (supporting). Emily N. Taylor: Conceptualization (equal); formal analysis (supporting); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (lead); writing-original draft (supporting).

DATA AVAILABILITY STATEMENT

Dryad doi: https://doi.org/10.5061/dryad.3xsj3txh9.

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REFERENCES

Aragón, P., Lobo, J. M., Olalla-Tárraga, M. A., & Rodriguez, M. A. (2010). The contribution of contemporary climate to ectothermic and endothermic vertebrate distributions in a glacial refuge. Global Ecology and Biogeography, 19(1), 40–49. https://doi.org/10.1111/j.1466-8238.2009.00488.x

Baird, T. A. (2004). Reproductive coloration in female collared lizards, Crotaphytus collaris, stimulates courtship by males. Herpetologica, 60(3), 337–348. https://doi.org/10.1655/03-17

Baird, T. A., McGee, A. A., & York, J. R. (2015). Responses to femoral gland secretions by visually adept male and female collared lizards. Ethology, 121(5), 513–519. https://doi.org/10.1111/eth.12365

Basson, C. H., Levy, O., Angilletta, M. J. Jr, & Clusella-Trullas, S. (2017). Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. Functional Ecology, 31(1), 856–865. https://doi.org/10.1111/1365-2435.12795

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1), 1–48. https://doi.org/10.18677/jss.v067i01

Baust, J. G. (1976). Temperature buffering in an arctic microhabitat. Annals of the Entomological Society of America, 69(1), 117–119. https://doi.org/10.1093/aesa/69.1.117

Bean, W. T., Stafford, R., Prugh, L. R., Butterfield, H. S., & Brashares, J. S. (2012). An evaluation of monitoring methods for the endangered giant kangaroo rat. Wildlife Society Bulletin, 36(3), 587–593. https://doi.org/10.1002/wsb.171

Burrow, A. L., Kazmaier, R. T., Hellgren, E. C., & Ruthven, D. C. III. (2001). Microhabitat selection by Texas horned lizards in southern Texas. The Journal of Wildlife Management, 65(4), 645–652. https://doi.org/10.2307/3803015

California Energy Commission (2019), Cal-Adapt: Exploring California’s climate change research. State of California. http://cal-adapt.org/

Cooper, W. E. Jr, DePerno, C. S., & Fox, S. F. (1996). Prey chemical discrimination and strike-induced chemosensory searching in lizards: Their absence in a crotaphytid lizard (Crotaphytus collaris) and a proposal for research in zoos. Zoo Biology, 15(3), 239–253. https://doi.org/10.1002/(SICI)1098-2361(1996)15:3<239:AID-ZOO4>3.0.CO;2-C

Downes, S., & Shine, R. (1998). Heat, safety or solitude? Using habitat selection experiments to identify a lizard’s priorities. Animal Behaviour, 55(5), 1387-1396. https://doi.org/10.1006/anbe.1997.0705
Scheffers, B. R., Brunner, R. M., Ramirez, S. D., Shoo, L. P., Diesmos, A., & Williams, S. E. (2014). Thermal buffering of microhabitats is a critical factor mediating warming vulnerability of frogs in the Philippine biodiversity hotspot. *Biotropica*, 45(5), 628–635. https://doi.org/10.1111/btp.12042

Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., & Evans, T. A. (2014). Microhabitats reduce animal’s exposure to climate extremes. *Global Change Biology*, 20(2), 495–503. https://doi.org/10.1111/gcb.12439

Sears, M. W., Angilletta, M. J. Jr, Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., Rusch, T. W., & Mitchell, W. A. (2016). Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, 113(38), 10595–10600. https://doi.org/10.1073/pnas.1604824113

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Cruz, M. V. S., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De La Riva, I. J., Sepúlveda, P. V., Rocha, C. F. D., Ibargüengoytía, N., Puntriano, C. A., Massot, M., ... Sites, J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328, 894–899. https://doi.org/10.1126/science.1184695

Souter, N. J., Michael Bull, C., & Hutchinson, M. N. (2004). Adding burrows to enhance a population of the endangered pygmy blue tongue lizard, *Tiliqua adelaidensis*. *Biological Conservation*, 116(3), 403–408. https://doi.org/10.1016/s0006-3207(03)00232-5

Steen, D. A., Linehan, J. M., & Smith, L. L. (2010). Multiscale habitat selection and refuge use of common kingsnakes, *Lampropeltis getula*, in southwestern Georgia. *Copeia*, 2010(2), 227–231. http://doi.org/10.1643/ce-09-092

Taylor, E. N., Diele-Viegas, L. M., Gangloff, E. J., Hall, J. M., Halpern, B., Massey, M. D., Rödder, D., Rollinson, N., Spears, S., Sun, B., & Telemecko, R. S. (2021). The thermal ecology and physiology of reptiles and amphibians: A user’s guide. *Journal of Experimental Zoology*, 335, 13–44. https://doi.org/10.1002/jezb.2396

U.S. Fish and Wildlife Service (1998). *Recovery plan for upland species of the San Joaquin Valley, California* (pp. 1–319). U.S. Fish and Wildlife Service.

Warrick, G. D., Kato, T. T., & Rose, B. R. (1998). Microhabitat use and home range characteristics of Blunt-nosed Leopard Lizards. *Journal of Herpetology*, 32(2), 183–191. https://doi.org/10.2307/1565295

Weaver, S. J., Westphal, M. F., & Taylor, E. N. (2021). Technology wish lists and the significance of temperature-sensing wildlife telemetry. *Animal Biotelemetry*, 9(1). http://doi.org/10.1186/s40317-021-00252-0

Westphal, M. F., Noble, T., Butterfield, H. S., & Lortie, C. J. (2018). A test of desert shrub facilitation via radiotelemetric monitoring of a diurnal lizard. *Ecology and Evolution*, 8(23), 12153–12162. https://doi.org/10.1002/ece3.4673

Zuliani, M., Ghazian, N., & Lortie, C. J. (2021). Shrub density effects on the community structure and composition of a desert animal community. *Wildlife Biology*, 2021(2), wlb.00774. https://doi.org/10.2981/wlb.00774

How to cite this article: Gaudenti, N., Nix, E., Maier, P., Westphal, M. F., & Taylor, E. N. (2021). Habitat heterogeneity affects the thermal ecology of an endangered lizard. *Ecology and Evolution*, 00, 1–14. https://doi.org/10.1002/ece3.8170