

HABITAT HETEROGENEITY AFFECTS THE THERMAL ECOLOGY OF THE FEDERALLY
ENDANGERED BLUNT-NOSED LEOPARD LIZARD

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TITLE: Habitat Heterogeneity Affects the Thermal Ecology
 of the Federally Endangered Blunt-Nosed Leopard
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ABSTRACT

Habitat Heterogeneity Affects the Thermal Ecology of the Federally Endangered Blunt-Nosed

Leopard Lizard

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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 but added a population of *G. sila* with no access to large shrubs to facilitate comparison of the thermal ecology of *G. sila* in shrubless and shrubbed populations. 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 population had higher midday body temperatures and therefore poorer thermoregulatory accuracy than *G. sila* from a shrubless population, suggesting that greater surface activity may represent a thermoregulatory tradeoff 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: *Gambelia sila*, thermoregulation, shrubs, shade, burrows, activity restriction, lizard

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TABLE OF CONTENTS

	Page
LIST OF FIGURES	viii
CHAPTER	
1. GENERAL INTRODUCTION.....	1
1.1. INTRODUCTION	2
1.2. MATERIALS AND METHODS	5
1.2.1. Field sites and study species	5
1.2.2. Microhabitat use	6
1.2.3. Temperature variables	7
1.2.4. Preferred body temperature and thermoregulatory accuracy	8
1.2.5. Hours of restriction and climatic projections	9
1.3. RESULTS.....	10
1.3.1. Microhabitat use	10
1.3.2. Thermoregulation	12
1.3.3. Hours of restriction and climatic projection	17
1.4. DISCUSSION	19
WORKS CITED.....	26

LIST OF FIGURES

Figure	Page
1. (A) A radio-collared Blunt-nosed Leopard Lizard (<i>Gambelia sila</i>) in the Carrizo Plain, California, USA. Photo by Emmeleia Nix. (B) The Shrubless (left) and Shrubbed (right) sites on the Elkhorn Plain in the Carrizo Plain National Monument.....	4
2. Microhabitat use of <i>Gambelia sila</i> at the Shrubbed site and the Shrubless site 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 the Shrubless site 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.	11
3. (A) Field-active body temperatures of <i>Gambelia sila</i> at a Shrubbed site and a Shrubless site in May, June, and July 2019; operative temperatures of three microhabitats (open sun, shade of plants, rodent burrows); the grey bar represents the lizard T_{set} range as measured in a thermal gradient; the dotted line is the panting threshold of <i>G. sila</i> (from Ivey et al., 2020). The shading around each line represents 1 SEM. (B) The percent of observations in which lizards used each of the three microhabitats at each site for each month between the hours of 0800 and 2000.....	13
4. Thermoregulatory accuracy (d_b) of <i>Gambelia sila</i> at a Shrubbed site (orange) and a Shrubless site (blue) during daylight hours over the course of their 3-month primary active season in 2019. The line at zero represents lizards thermoregulating within T_{set} ; positive values mean that lizards are thermoregulating above the upper bound of their T_{set} range; negative values mean that lizards are thermoregulating below the lower bound of their T_{set} range. The shading around each line represents 1 SEM. During the hottest months of June and July, lizards from the Shrubbed site had poorer thermoregulatory accuracy than lizards from the Shrubless site.	16

5. Hours of restriction from using specific microhabitats for <i>Gambelia sila</i> 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 the Shrubbed site experienced about one more hour of restriction than lizards at the Shrubless site.	18
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Chapter 1

GENERAL INTRODUCTION

The Blunt-Nosed Leopard Lizard (*Gambelia sila*) is a federally endangered heliothermic lizard whose distribution is currently about 10% of its value prior to being listed as federally endangered in 1967. They once spanned across California's San Joaquin Valley, but were forced to retreat to the few remaining natural areas as agriculture and oil fields began to take over California's Central Valley. The Carrizo Plain National Monument is the largest remaining relatively undisturbed San Joaquin Desert habitat and has been the location of previous studies investigating *G. sila*'s ecology. My study seeks to further understand their ecology to inform management efforts for the lizards' continued protection in the areas where they still persist. A population of lizards in the Carrizo Plain's higher-elevation Elkhorn Plain has been studied in the past few years; notably, their thermal ecology was evaluated in 2018 and the authors suggested that lizards may be able to use large shrubs to buffer the effects of the very hot ambient temperatures that are characteristic of their active season in the Carrizo Plain. My study was intended as a follow-up to this study, conducted on lizards at that same site, and additionally on a population of lizards at a nearby site with no large shrubs present to understand the importance of shrubs for *G. sila*'s thermoregulation. It is vital to understand the role these shrubs play in *G. sila*'s thermal ecology because artificial shrubs could potentially be used as a management action to help these lizards survive the projected rising temperatures that they will inevitably experience in the near future. These lizards are a beautiful and charismatic component of the San Joaquin Desert ecosystem, and a solid understanding of which components of their environment are crucial for their thermoregulation is necessary to make informed decisions about how to further protect this species as global ambient temperatures continue to rise.

1.1. INTRODUCTION

Many organisms are threatened by the projected increase in global temperatures. As ectotherms, reptiles will be disproportionately threatened because their body temperatures are dependent on the temperature of their environment (Aragón et al. 2010). Models estimate up to 90% of lizard populations may be extirpated in as little as 30 years from now (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. 2020). 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 (Germano et al. 2011), where already high temperatures are becoming even more extreme (Ivey et al. 2020). Adult *G. sila* are primarily only active for a few short months (late April through mid-July) (Montanucci 1965, Germano & Williams 2005), 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* (Filazzola 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 like *G. sila*. Advances in the sizes and technology of radio telemetry transmitters now allow for ample data collection on physiological aspects of small animals (Weaver et al. in press). 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 and suggested that shrubs allow *G. sila* to remain above ground 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 with a comparison between two sites, we studied *G. sila* in 2019 at the same site as Ivey et al. (2020), hereafter called the Shrubbed site, and added a second nearby site where *G. sila* had virtually no access to shrubs (Shrubless site). 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 above-ground 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 as well as other sensitive San Joaquin Desert species from rising temperatures in some of the hottest, driest parts of the continent.



Figure 1. (A) A radio-collared Blunt-nosed Leopard Lizard (*Gambelia sila*) in the Carrizo Plain, California, USA. Photo by Emmeleia Nix. (B) The Shrubless (left) and Shrubbed (right) sites on the Elkhorn Plain in the Carrizo Plain National Monument.

1.2. MATERIALS AND METHODS

1.2.1. Field sites and study species

A pair of sites (a Shrubbed site with *E. californica* and other smaller perennial shrubs, and a Shrubless site with no *E. californica* and very few other shrubs) were selected on the Elkhorn Plain within the Carrizo Plain National Monument in California, USA (Figure 1b). The Shrubless site was selected because lizards had been seen in the area previously, and it was only 6.5km away from the Shrubbed site where we have previously collected data. The sites are similar in size (400m²), as well as climate and elevation. Microhabitat use and shrub association of lizards at the Shrubbed site were studied in 2016 (Westphal et al., 2018), and field-active body temperatures of lizards were continuously recorded there in 2018 (Ivey et al., 2020). *Gambelia sila* at the Shrubbed site had access to *D. ingens* burrows as well as ample shade provided primarily by large *E. californica* shrubs and smaller perennials like *Isocoma acradenia* and *Gutierrezia californica*, and also some shade provided by small annual plants like *Amsinckia* sp. and nonnative grasses. In contrast, lizards at the nearby Shrubless site could make use of burrows, but unlike the Shrubbed site there are no large shrubs and only extremely rare spots of above-ground shade provided by very sparse *I. acradenia*, *G. californica*, and *Astragalus* sp. (mostly *A. lentiginosus*, sometimes *A. oxyphysus*), in addition to small annual forbs and grasses. The Shrubless site had very few perennial shrubs, only a few in the entire site, and notably these shrubs were only used by a total of two lizards whose territories happened to be in an area that included these shrubs. Therefore, use of shrub-provided shade by lizards at the Shrubless site was extremely rare (see Results). Burrows at both sites 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 the Shrubbed site only.

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, $\pm 0.5\text{mm}$), and mass ($\pm 1\text{g}$). Lizards were fitted with VHF temperature-sensitive radio-transmitter collars with 16cm 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 individual lizards (N = 22 Shrubbed, N = 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; July Shrubbed N=16, Shrubless N=15.

1.2.2. Microhabitat use

We tracked *G. sila* using a VHF receiver (R-100 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, or 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 sun, or underground in a burrow. A lizard was designated as underground in a burrow if the observer could not see it; sometimes lizards sat at the entrances of burrows but this was categorized as the open because portions of their body, notably the temperature-sensitive radio collar, were in the sun. All of the lizards categorized as underground were not visible from the burrow mouth. 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 within 10m along four 100m randomly placed transects at each site. We compared the burrow densities at the Shrubbed and Shrubless sites with a Student's t-test in R.

1.2.3. Temperature variables

At the center of each site, we installed a stationary 10ft tall solar-powered (Tycon RemotePro 2.5W 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 determined the range for continuous, gap-free data collection with this antenna to be approximately 300m. 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. 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.

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 the open sun, in the shade, and inside burrows, using the same models as Ivey et al. (2020). Models consisted of 1in (2.5cm) diameter copper pipes capped with PVC and spray-painted matte gray. 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. sika* resting posture. Each model housed a Thermochron iButton (DS1921G-F5) programmed to record temperature every hour, on the hour. The pipes were filled with water to mimic a body cavity (Dzialowski 2005), and plumber's tape was used to waterproof the seal before the caps were screwed on. 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 0.5m 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 sun during all 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, 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_e) in analyses (see below), where T_e represent the effective microhabitat temperatures available to *G. sila*.

1.2.4. Preferred body temperature and thermoregulatory accuracy

As *G. sila* aestivation approached in mid-July, we re-captured and re-processed 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 x 20 x 25cm) 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 5SRTC-TT-K-40-72, Omega Engineering, UK) in their cloacae recording body temperature every 10 minutes for three hours. These data were recorded on a data logger (model RDXL4SD, Omega Engineering, Egham, Surrey, UK), and only the last hour of data was used for analysis. While longer time periods for assessing T_{set} are ideal, *G. sila* can only be held captive for a short period of time due to their endangered status.

We calculated average T_{set} 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_{set} range. Since there was no significant difference in T_{set} between the two populations (see Results), we used the mean T_{set} IQR of all lizards for the following analyses. We calculated lizard thermoregulatory accuracy (d_b) by subtracting the mean

T_{set} 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 were higher or lower than T_{set} range. Lizard T_b was also compared to the panting threshold (T_{pant}) of *G. sila*, which is a measure of upper thermal tolerance that Ivey et al. (2020) measured in 2018. It was not possible to measure the critical thermal maximum of *G. sila* because their endangered status precluded heating them to temperatures close to their upper lethal threshold. T_{pant} therefore represents a conservative measure of upper thermal tolerance. All d_b values for each lizard were averaged by hour per day from 0700 to 2000 (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 the Shrubbed and Shrubless sites, d_b values were further averaged to give one value per lizard per month, and we ran a multi-factor ANOVA with d_b as the response variable; site, month, and the site by month interaction as fixed factors; and lizard ID as a random factor nested within site, using JMP (SAS Institute Inc., v. 14.3, 2018).

1.2.5. Hours of restriction and climatic projections

We compared temperatures from the physical models (T_e) to *G. sila* T_{set} and T_{pant} (the latter from Ivey et al. 2020) each hour of the day for each month to calculate the number of hours in a day that a given microhabitat would be too hot (i.e., exceed either T_{set} or T_{pant}) for a lizard. We designated hours of restriction as “basking restriction” when temperatures in the open sun were too hot and lizards therefore must be in shade or in burrows; “above-ground 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 the Shrubbed site); and “total restriction” when all three microhabitats including burrows are too hot (Ivey et al. 2020).

Each of these hours of restriction variables were 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 scenario 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).

1.3. RESULTS

1.3.1. Microhabitat use

From May through mid-July 2019, we collected 1,148 individual telemetry observations of *G. sila* at the Shrubbed site and 1,019 observations of lizards at the Shrubless site. 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 the Shrubless site found some shade from annual plants and very rare shrubs to use, they collectively spent very little time in the shade throughout the active season. In June and July, lizards from the Shrubless site spent 46% and 57% of their observed time inside burrows, compared to 31% and 43% for lizards at the Shrubbed site. The probability that lizards at the Shrubless site would be found underground in *D. ingens* burrows instead of above-ground was higher than that for lizards at the Shrubbed site ($z=4.35$, $p<0.001$) throughout the season. Burrow density was not significantly different between the two sites (Shrubbed: 35.83 ± 4.71 burrows/100m, Shrubless: 44.67 ± 6.26 burrows/100m; $t = -1.36$, $p = 0.23$).

The woody perennial shrubs most commonly used for shade by lizards at the Shrubbed site were *G. californica*, followed by *I. acradenia*, *E. californica*, unidentifiable dead small shrubs which likely were either *I. acradenia* or *G. californica*, and a single individual had access to and used *E. fasciculatum* (Figure 2b). In May, when annuals were plentiful, lizards at the Shrubbed site 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.

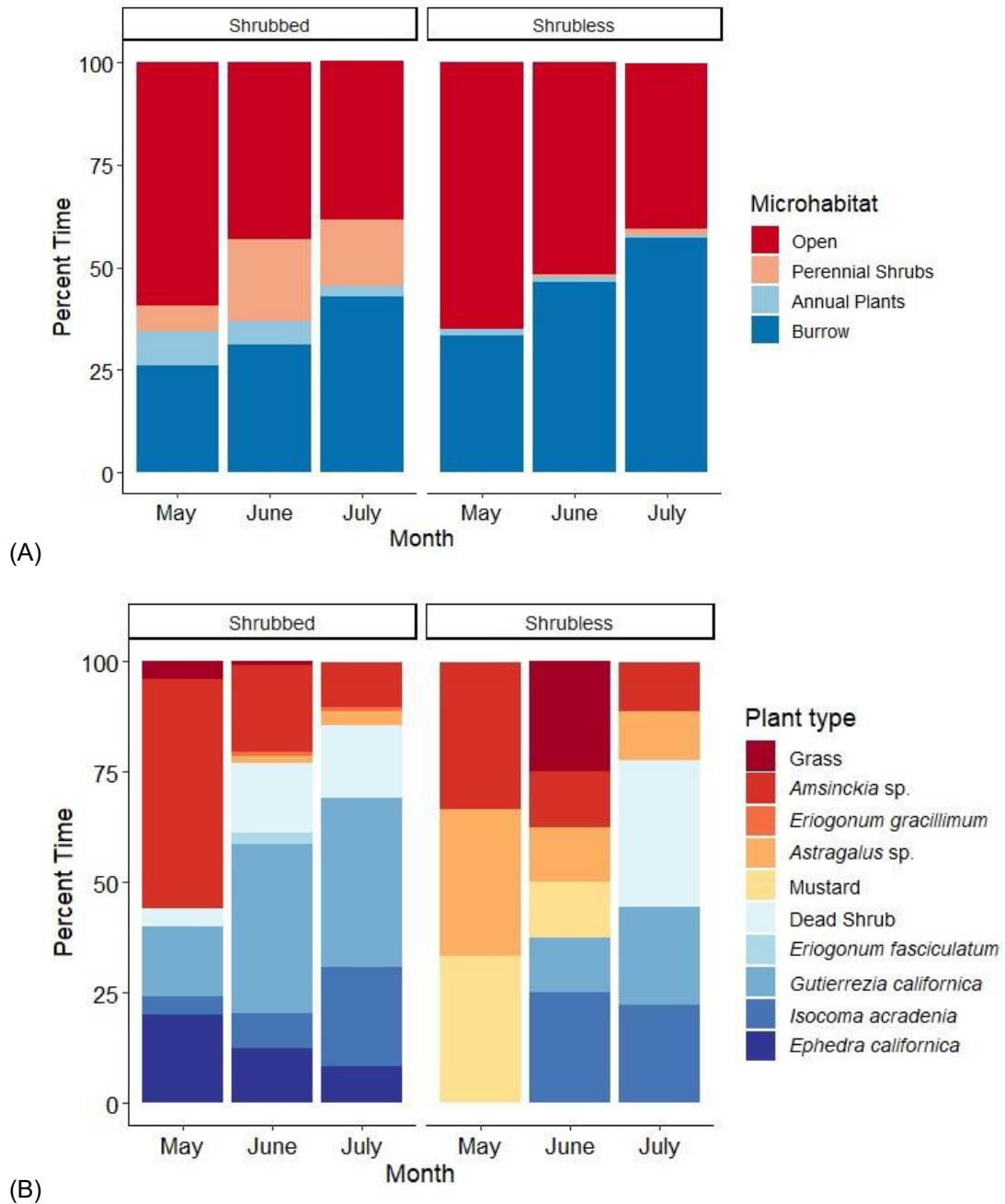


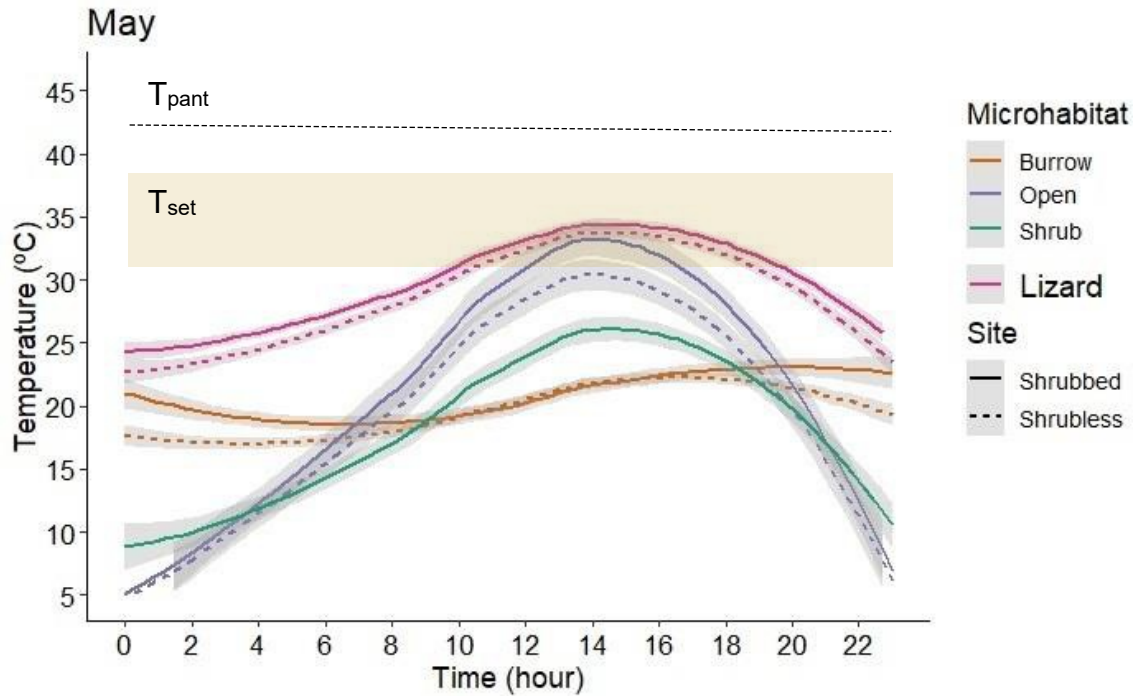
Figure 2: Microhabitat use of *Gambelia sila* at the Shrugged site and the Shrubless site over the course of their 3-month primary active season in 2019, showing (A) percent of time spent in the open sun, in the shade of annual and perennial plants, and in rodent burrows, and (B) use of plant species for shade at each site. Lizards at the Shrubless site 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.

1.3.2. Thermoregulation

The mean T_{set} for *G. sila* at the Shrubbed site was 34.1 °C with IQR of 32.3-36.8 °C, and mean T_{set} for lizards at the Shrubless site was 35.0 °C with IQR of 35.1-38.5 °C. Because these values were not significantly different from one another ($t = -0.89$, $p = 0.38$), 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 mean 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 the open sun exceeded T_{pant} for several hours while the shrub and burrow T_e stayed below T_{pant} (Figure 3). T_b of lizards at the Shrubless site were slightly lower than at the Shrubbed site but not significantly so (site: $F = 2.74$, $df = 1$, $p = 0.1$; month: $F = 243.15$, $df = 2$, $p < 0.0001$; site by month interaction: $F = 0.27$, $df = 2$, $p = 0.76$; Figure 3). As the day progressed, lizards moved from burrows to the open, and then retreated back into burrows typically in the late afternoon when temperatures were especially high (Figure 3). On average, lizards at the Shrubless site thermoregulated more accurately than lizards from the Shrubbed site (site: $F = 77.39$, $df = 1$, $p < 0.0001$; month: $F = 193.71$, $df = 2$, $p < 0.0001$; site by month interaction: $F = 0.12$, $df = 2$, $p = 0.89$; Figure 4). In May, lizards at both sites thermoregulated fairly accurately (d_b near 0 in the middle of the day), but lizards at the Shrubbed site thermoregulated more accurately than lizards from the Shrubless site (Figure 4). In June and July, *G. sila* at the Shrubless site thermoregulated more accurately than lizards at the Shrubbed site. During these hot months, d_b of lizards at the Shrubbed site was better in the mornings and evenings but poorer during the day, whereas lizards at the Shrubless site kept their d_b closer to 0 during the day by staying in burrows more often than lizards at the Shrubbed site.

(A)



(B)

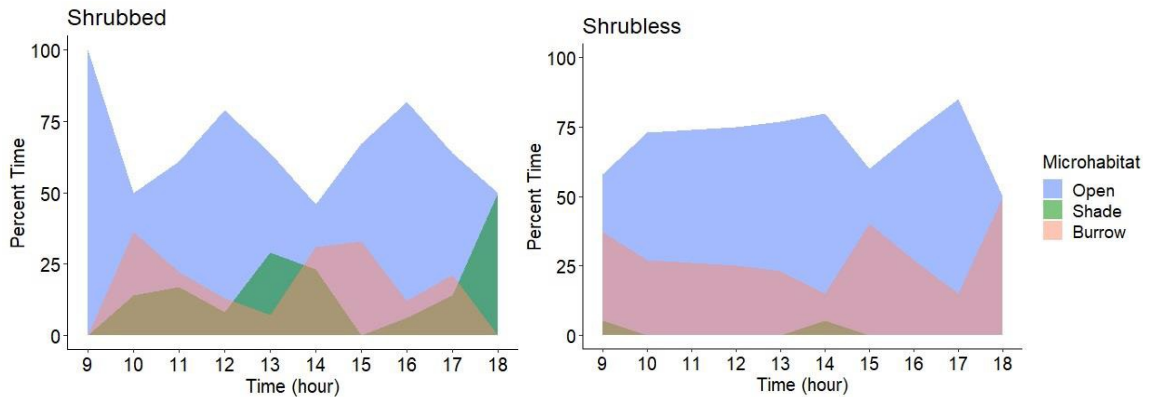


Figure 3: (A) Field-active body temperatures of *Gambelia sila* at a Shrubbed site and a Shrubless site in May, June, and July 2019; operative temperatures of three microhabitats (open sun, shade of plants, rodent burrows); the grey bar represents the lizard T_{set} range as measured in a thermal gradient; the dotted line is the panting threshold of *G. sila* (from Ivey et al., 2020). The shading around each line represents 1 SEM. (B) The percent of observations in which lizards used each of the three microhabitats at each site for each month between the hours of 0800 and 2000.

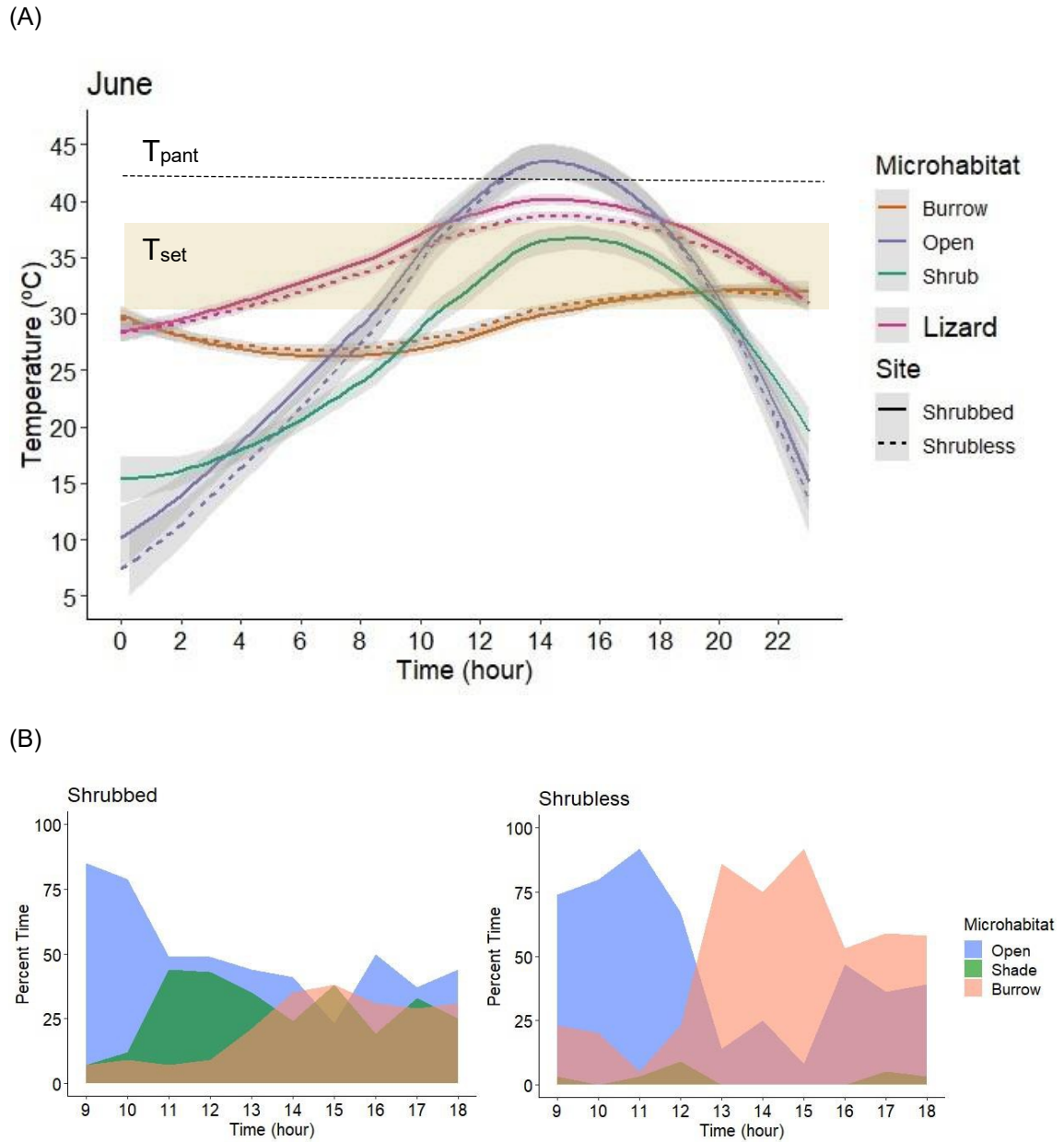


Figure 3: (A) Field-active body temperatures of *Gambelia sila* at a Shrubbed site and a Shrubless site in May, June, and July 2019; operative temperatures of three microhabitats (open sun, shade of plants, rodent burrows); the grey bar represents the lizard T_{set} range as measured in a thermal gradient; the dotted line is the panting threshold of *G. sila* (from Ivey et al., 2020). The shading around each line represents 1 SEM. (B) The percent of observations in which lizards used each of the three microhabitats at each site for each month between the hours of 0800 and 2000.

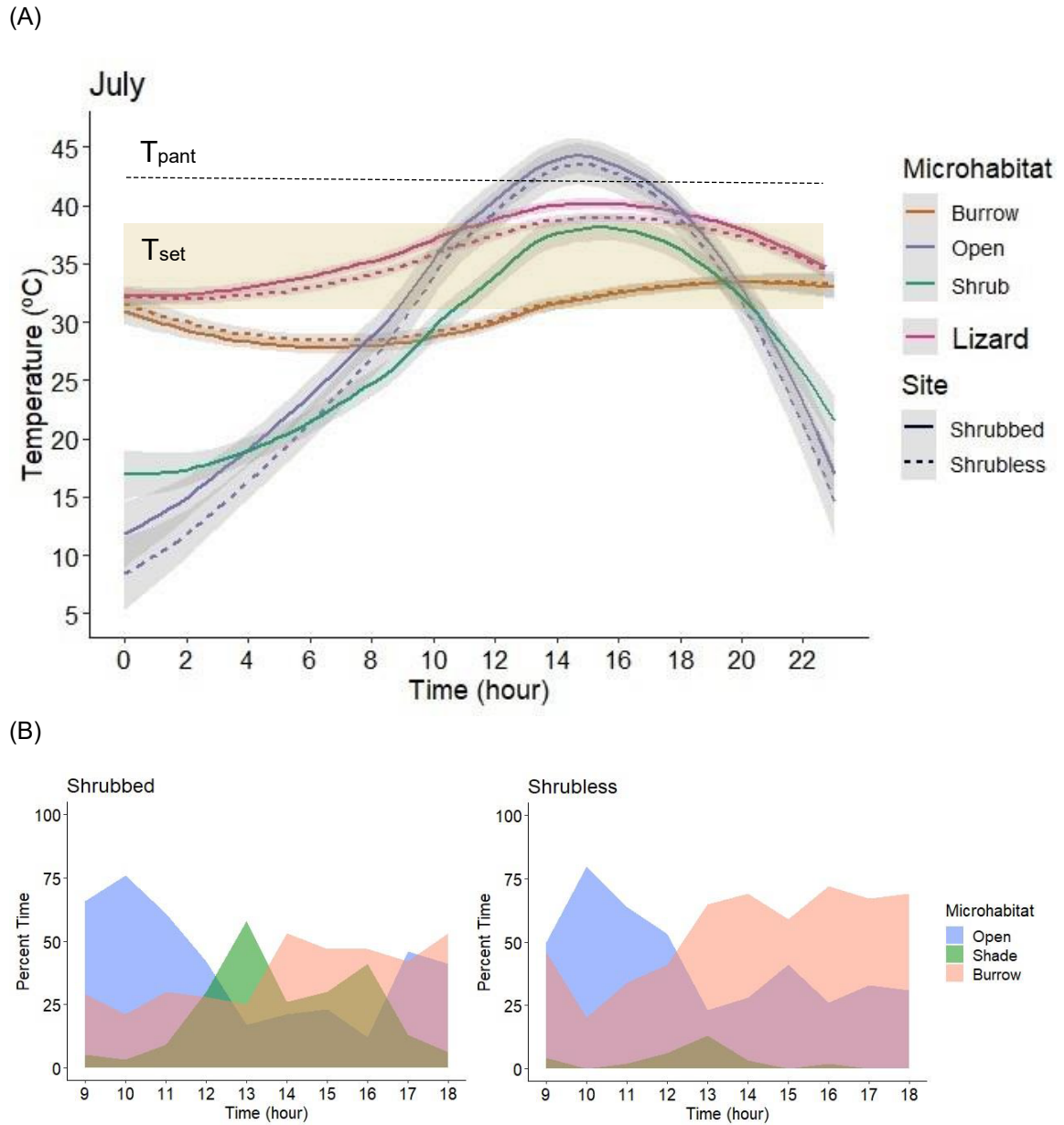


Figure 3: (A) Field-active body temperatures of *Gambelia sila* at a Shrubbed site and a Shrubless site in May, June, and July 2019; operative temperatures of three microhabitats (open sun, shade of plants, rodent burrows); the grey bar represents the lizard T_{set} range as measured in a thermal gradient; the dotted line is the panting threshold of *G. sila* (from Ivey et al., 2020). The shading around each line represents 1 SEM. (B) The percent of observations in which lizards used each of the three microhabitats at each site for each month between the hours of 0800 and 2000.

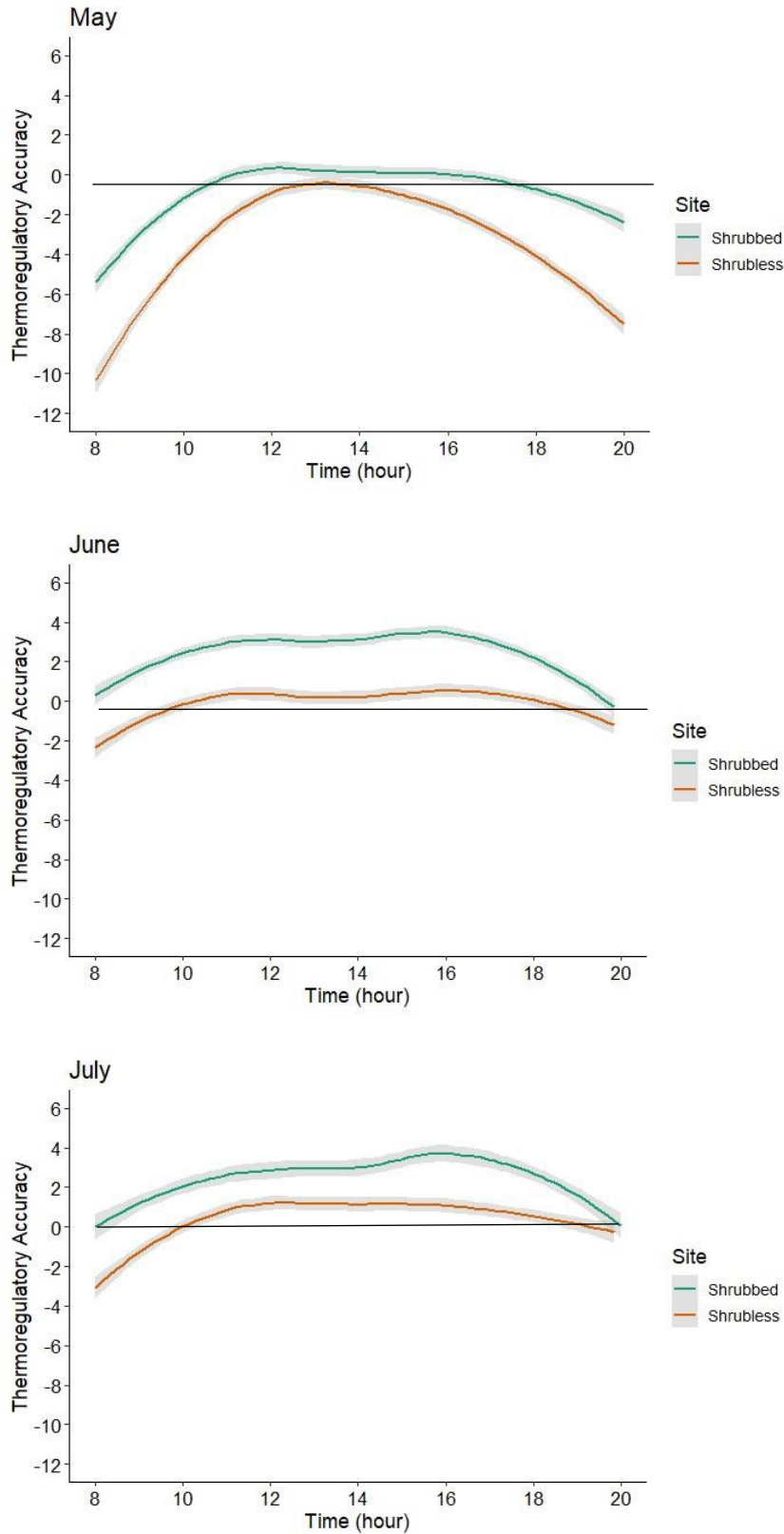


Figure 4: Thermoregulatory accuracy (d_b) of *Gambelia sila* at a Shrubbed site (orange) and a Shrubless site (blue) during daylight hours over the course of their 3-month primary active season in 2019. The line at zero represents lizards thermoregulating within T_{set} ; positive values mean that lizards are thermoregulating above the upper bound of their T_{set} range; negative values mean that lizards are thermoregulating below the lower bound of their T_{set} range. The shading around each line represents 1 SEM. During the hottest months of June and July, lizards from the Shrubbed site had poorer thermoregulatory accuracy than lizards from the Shrubless site.

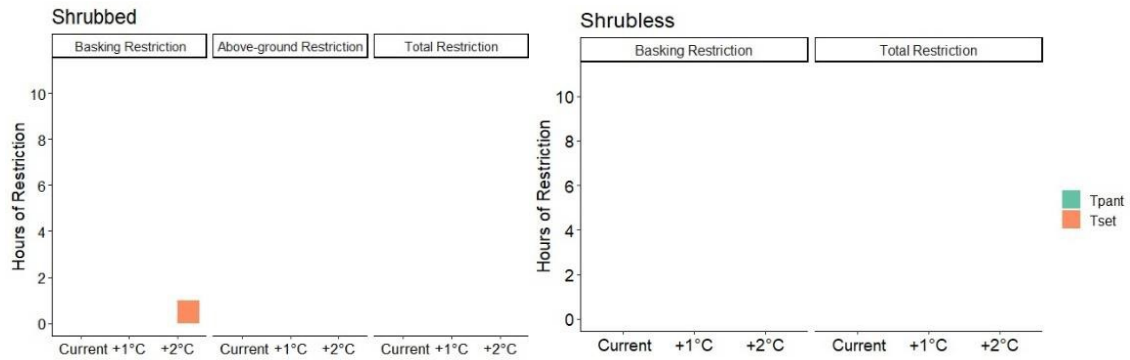
1.3.3. Hours of restriction and climatic projections

Because May temperatures are so mild, *G. sila* does not currently experience any hours of restriction from using various microhabitats during daylight hours in May (Figure 5). However, in June and July, *G. sila* were restricted from basking in the open sun (basking restriction) for 8-11 daylight hours because T_b would exceed T_{set} , or for 6-8 daylight hours because T_b would exceed T_{pant} (Figure 5). In June and July, *G. sila* at the Shrubbed site experience one more hour of basking restriction than lizards at the Shrubless site (Figure 5). Lizards at the Shrubbed site are restricted from being above ground at all (above-ground restriction) for 3 of the 12 hours in June and for 8 hours in July because T_b would exceed T_{set} . Currently, T_e inside burrows at both sites never exceeded T_{set} or T_{pant} , and T_e under shrubs at the Shrubbed site never exceeded T_{pant} .

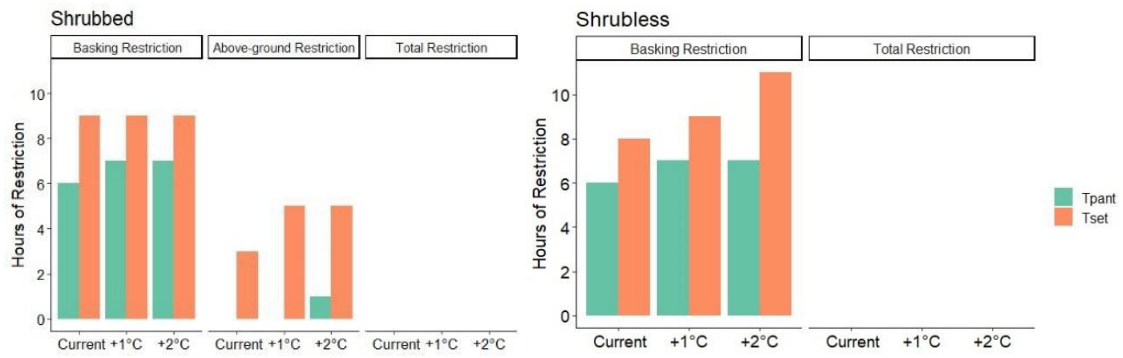
As expected, adding 1°C and 2°C to the T_e data resulted in additional projected hours of restriction associated with climate change for both populations in June and July (Figure 5).

Lizards at the Shrubbed site will be restricted from basking in the sun and staying within their T_{set} range for 9-10 daylight hours, and lizards at the Shrubless site would be similarly restricted for 8-11 hours. Notably, lizards at the Shrubbed site should still be able to stay above ground for several hours under future climate change scenarios because of their access to the shade of a shrub, while lizards at the Shrubless site do not have this option. Even under conditions with 1°C or 2°C increases in all microhabitats, temperatures in burrows should remain low enough for lizards to stay below their T_{set} .

May



June



July

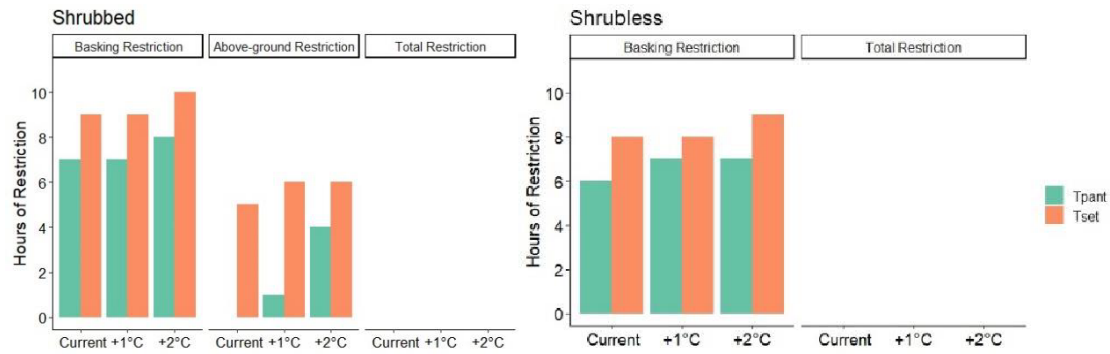


Figure 5: Hours of restriction from using specific microhabitats for *Gambelia sila* at a Shrubbed Site and a Shrubless Site over the course of their 3-month primary active season in 2019, calculated as the number of daylight hours in which microhabitat operative temperature T_e exceeds T_{set} (orange) 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 the Shrubbed site experienced about one more hour of restriction than lizards at the Shrubless site.

1.4. DISCUSSION

Gambelia sila is an endangered heliothermic lizard that is threatened by rising temperatures. Because previous research (Ivey et al. 2020) suggested that shrubs provide shade that allows *G. sila* to remain above ground when it is too hot in the open sun, we directly assessed the influence of shrubs on their thermoregulation by comparing thermal variables in a population with access to shrubs to a population with virtually no access to shrubs. As predicted, we found that lizards that had access to shrubs spent more time above-ground than those that did not, as lizards at the Shrubless site spent more time inside *D. ingens* burrows. However, unexpectedly, 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 above-ground. 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 the Shrubless site was not the result of more available burrows. Instead, lizards at the Shrubless site likely have to limit their time spent above-ground because they would become too hot in the open sun, while lizards at the Shrubbed site can retreat to the shade of a shrub when the open microhabitat becomes too hot. Like Ivey et al. (2020), we found that lizards will be further constrained from being active above ground 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 above ground 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.

The presence of shrubs allowed *G. sila* to spend more time above-ground, 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 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 (Moore et al. 2018, Fenner et al. 2012, Grillet 2010). Models suggest that lizards will need to go deep into burrows to deal with climate change (Kearney et al 2020). However, above-ground shade may also be critical to facilitate feeding, mating, and other behaviors in species like *G. sila*. Crotaphytid lizards like *G. sila* hunt their prey using visual cues, and lack lingually mediated prey chemical discrimination (Cooper et al. 1996), suggesting that most hunting indeed occurs above-ground. Male crotaphytids rely on bright mating coloration to find mates (Baird, 2004), with chemosensory cues from femoral secretions appearing to play secondary roles such as permitting female assessment of male quality (Baird et al., 2015). Shrubs may therefore 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 above ground at the Shrubless site in terms of hunting success or fitness. Such a study would further elucidate the importance of shrubs in allowing above-ground activity in *G. sila*.

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, Hacking et al. 2013, Germano et al. 2001). Notably, lizards at the Shrubless site always used shade far less often than lizards at the Shrubless site. However, our study shows that when shrubs are not available, *G. sila* can use annuals for shade. In addition, we occasionally observed *G. sila* climbing grasses, especially at the Shrubless site, 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 the Shrubless site than those at the Shrubbed site (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 the Shrubless site, which otherwise had only very sparse *I. acradenia* and *G. californica* and no *E. californica*. Surprisingly, *E. californica* was not the predominant shrub used by *G. sila* at the Shrubbed site in our study, which used *I. acradenia* and *G. californica* more often. Numerous studies at the Shrubbed site 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, Filazzola et al. 2017), showed that *G. sila* select for large shrubs like *E. californica* more than what would be expected based on shrub density (Westphal et al. 2018), and that *G. sila* scat is found more frequently under *E. californica* canopies than the open (Filazzola et al. 2017). Our study followed a relatively wet winter, and the smaller *I. acradenia* and *G. californica* shrubs may not have been 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 (Ivey et al. 2020, Westphal et al. 2018, Filazzola 2017). 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 the Shrubbed site seemed to use smaller perennial shrubs like *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 highly visually oriented lizards to better see prey, predators, mates, and rivals.

Thermoregulatory accuracy was higher for lizards at the Shrubless site than at the Shrubbed site, 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_e in the open was higher at the Shrubbed site than at the Shrubless site (Figure 3), even though we chose these nearby sites as “matched” sites. Models inside burrows also warmed up faster in the morning at the *Shrubbed Site* than at the *Shrubless Site* in May, but not in June or July (Figure 3). When studying an endangered species with sparse populations, we have only a small number of populations available, precluding us from replicating observations at multiple shrubbed and shrubless sites. 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 the Shrubless site is that they spent more time in burrows during the middle of the day, where T_e is closer to T_{set} , while lizards at the Shrubbed site spent more time above ground, both in the open sun and in the extensive shade that is unavailable at the Shrubless site. Perhaps lizards at the Shrubbed site could risk operating at T_b higher than their T_{set} during the day because they have an available above-ground buffer in the form of ample shade, while lizards at the Shrubless site have to limit their time spent above-ground because they cannot risk becoming too hot before retreating into a burrow. Simulated models indicated that lizards are expected to conserve energy by thermoconforming in a more homogeneous landscape like the Shrubless site (Basson et al. 2017); the lizards at the Shrubless site indeed spent less time in the sun and therefore were more thermoconforming than lizards at the Shrubbed site. 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. Finally, some individual lizards had high leverage on thermoregulatory accuracy results, but were kept in the final analysis because there was no explanation for why they were outliers other than individual variation. There was an especially bright orange (breeding color) female at the Shrubbed site that had much lower body temperature data for all three months than other

lizards, likely because she was often observed inside burrows, possibly because she was nesting more. In June and July, there were two males at the Shrubbed site that had high body temperatures, which may be skewing the lizard temperatures for that site. One of these males was large and especially bright orange, so he may have been spending more time outside patrolling his territory.

The lack of shrubs at the Shrubless site may have consequences that extend beyond thermoregulation. More *G. sila* at the Shrubless site (N = 6) were lost to probable predation than at the Shrubbed site (N = 1). Indeed, there were more confirmed mortalities (dead lizard found with collar) at the Shrubless site (N = 4) than at the Shrubbed site (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 the Shrubless site were found with lizard stomach and 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 conclusions, these data suggest that lizards at the Shrubless site might experience higher predation pressure than those at the Shrubbed site. Lack of large shrubs like *E. californica* may allow birds of prey or other visually oriented predators like snakes to more easily see and capture lizards on the desert floor. Predation may therefore be an additional reason why *G. sila* at the Shrubless site spent more time underground in rodent burrows than those at the Shrubbed site. 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 (Martin & Lopez 1998). In accordance with this idea, *G. sila* were observed using *E. californica* for predator avoidance in our study and in others (Montanucci 1965, Filazzola 2017, Westphal et al. 2018).

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. 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 the Shrubbed site would have on average one more hour of basking restriction than lizards at the Shrubless site. These data present an interesting conundrum: *G. sika* at the Shrubless site do not have above-ground 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 the Shrubless site suggest that lizards there may actually experience fewer hours of restriction from basking in the sun than lizards at the hotter Shrubbed site. However, lizards at the Shrubbed site still have the option of staying above-ground for more hours of the day than lizards at the Shrubless site because they can retreat to the cooler shade of shrubs. Further increases in the number of hours of basking restriction or above-ground 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. Luckily, our data suggest that *G. sika* are unlikely to be restricted from all their microhabitats even after a 2 °C increase. Also, our projections merely add 1-2 °C to current T_e , whereas certain microhabitats might actually warm at a slower rate, providing thermal buffers (González-del-Piiego 2020, Scheffers et al. 2014, Scheffers et al. 2014, Baust 1976). A more robust prediction would take into account these differences in warming rate for each microhabitat compared to ambient temperature, which would likely be even 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_b 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} .

In conclusion, we found that *G. sika* without access to shrubs are not necessarily in greater danger of overheating or losing hours of activity, as lizards at the Shrubless site thermoregulated closer to their T_{set} than lizards from the Shrubbed site. While shrubs may play an important role in lizard thermoregulation, lizards at the Shrubless site 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 perhaps even more important. In addition to deploying artificial shade structures (Ghazian 2020), ensuring the continued presence of *D. ingens* may be essential in securing *G. sila* persistence. Burrows excavated by ecosystem engineers like *D. ingens* are often critical to the survival of other community members (Prugh & Brashares 2012, Pike & Mitchell 2013). Additionally, our data suggest that shrubs could be important in protecting *G. sila* from avian predators like ravens, further underscoring the notion 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 help 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.

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