

Gimme Shelter: Thermally-mediated refuge site selection by Gila monsters (*Heloderma suspectum*)

By

Brandon Brown

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of  
Master of Science

Austin Peay State University  
August 2021

Thesis Committee:

Dr. Christopher Gienger, Committee Chair

Dr. Catherine Haase

Dr. Rebecca Johansen

Brandon Brown

Approved:

Handwritten signature of C.M. Gienger in black ink.

---

Dr. C.M. Gienger, Committee Chair

Handwritten signature of Catherine Haase in black ink.

---

Dr. Catherine Haase, Committee Member

Handwritten signature of Rebecca Johansen in black ink.

---

Dr. Rebecca Johansen, Committee Member

Handwritten signature of Chad Brooks in blue ink.

---

Dr. Chad Brooks, Associate Provost and Dean, College of Graduate Studies

### Statement of Permission to Use

In presenting this thesis in partial fulfillment of the requirements for the Master of Science at Austin Peay State University, I agree that the library shall make it available to borrowers under the rules of the library. Brief quotations from this thesis are allowable without special permission, provided that accurate acknowledgement of the source is made. Permissions for extensive quotation or reproduction of this thesis may be granted by my major professor, or in his/her absence, by the Head of the Interlibrary Services when, in the opinion of either, the proposed use of the material is for scholarly purposes. Any copying or use of the material in this thesis for financial gain shall not be allowed without my written permission.

Brandon Brown

06/29/2021

## ACKNOWLEDGMENTS

We thank Jason Jones and the Nevada Department of Wildlife, as this research would not have been possible without them. We also thank Jocelyn Stalker for her help in radio tracking the Gila monsters. This research was supported by the Center of Excellence for Field Biology at Austin Peay State University and the Clark County Nevada Desert Conservation Program.

## ABSTRACT

The Gila monster (*Heloderma suspectum*) is a desert lizard which experiences strong above-ground thermal constraints throughout its range and copes with suboptimal environmental temperatures by retreating to sub-surface refuge sites. We addressed the hypothesis that refuge sites selected by Gila monsters would have higher thermal quality and provide more thermally stable regimes than sites not used as refuge. We measured the thermal properties of 48 selected shelters, each matched with two control shelters; a potential shelter having similar physical characteristics to the selected shelter but not observed to be used as refuge, and a random shelter, in which physical attributes were not controlled for, but still having the size and depth to be used as sub-surface refuges. We found that overall mean temperature did not differ among the three shelter types. In addition, random shelters had more time within the preferred thermoregulatory range of the Gila monster ( $T_{set}$ ) when compared to potential shelters but shelters that were selected by Gila monsters did not differ from the other shelter types in the total amount of time spent within  $T_{set}$ . Over the course of the activity season, selected shelters deviated less from  $T_{set}$  and were more thermally stable than potential or random shelters. Our results also indicate a temporal shift in thermally-mediated shelter selection. Early in the activity season (April), selected refuge sites had temperatures within  $T_{set}$  for longer when compared to potential shelters. Later in the activity season (June and July) when above-ground temperatures were higher and potentially lethal, selected shelters had higher thermal stability and temperatures that were closer to  $T_{set}$  than other shelter types. Overall, our results indicate that shelter-selection in Gila monsters is thermally-mediated in ways that change over the course of the activity season, and that using biologically informative metrics is important in measuring thermal suitability of refuge sites in the field.

## TABLE OF CONTENTS

INTRODUCTION .....	1
METHODS	
Study site.....	4
Experimental Design.....	5
Thermal Quality .....	6
Thermal Stability .....	7
Statistical Analyses .....	8
RESULTS	
Shelters.....	9
Thermal Quality .....	9
Thermal Stability .....	11
Occupancy and Usage.....	12
DISCUSSION.....	13

## LIST OF TABLES AND FIGURES

TABLE 1.....	18
FIGURE 1 .....	19
FIGURE 2 .....	20
FIGURE 3 .....	21
FIGURE 4 .....	22
FIGURE 5 .....	23
FIGURE 6 .....	24
FIGURE 7 .....	25
FIGURE 8 .....	26
FIGURE 9 .....	27
FIGURE 10 .....	28

## **Introduction:**

Refuge site selection plays a crucial role in the survival of many organisms (Christian et al., 1984; Huey et al., 1989; Huey, 1991). Refuges function in predator avoidance and escape (Downes and Shine, 1998; Cooper and Frederick, 2007; Holbrook et al., 2008; Weisel et al., 2015) and offer physical protection from unsuitable environmental conditions (Holbrook et al., 1990; Ebeling and Hixon, 1991; Webb and Shine, 2000). In fossorial and reclusive species refuge sites may also provide opportunities for conspecific interactions and serve as the primary location of mating and nesting activities (Eggleston and Lipcius, 1992; Pereira et al., 2019).

Microclimate gradients within refuge sites provide conditions that permit behavioral thermoregulation (Huey, 1982; Kearney, 2002). Thermoregulation influences the physiology, ecology, and reproduction of most ectotherms (Huey and Stevenson, 1979; Huey, 1982; Huey and Kingsolver, 1989), which attempt to maintain their body temperatures within a preferred range, putatively to permit optimal performance of essential bodily functions (Berk and Heath, 1975; Barber and Crawford, 1977; Hertz et al., 1993). Homeostatic mechanisms such as shivering (Vinegar, 1968; Heinrich and Pantle, 1975; Harlow & Grigg, 1984) and counter-current heat exchange (Bernal et al, 2001; Wegner et al., 2015) are used by some ectothermic species to keep body temperatures within, or closer to this preferred range. Ectotherms can also behaviorally thermoregulate (Cowles and Bogert, 1944; Bogert 1949) through activities such as basking (Heinrich and Pantle, 1975; Barton et al, 2014; Stanton-Jones et al., 2018), positional adjustments (Barton et al., 2014), and use of refuge sites (Christian et al., 1983).

Refuges routinely serve as a critical thermal escape from stressful or lethal temperatures (Kearney et al., 2009; Vasconcelos et al., 2012; Bonnet et al., 2013; Moore et al., 2018). Sites having higher thermal quality (more time within the preferred temperature range of a particular



species or temperatures that deviate less from that range) or greater thermal stability may be intentionally sought out when environments experience high levels of thermal fluctuation, especially when temperatures exceed critical thermal limits (Barnes et al., 1996; Kearney et al., 2009; Rowland et al., 2017; Nordberg and Cobb 2017). In desert environments, high temperatures impose strong daily and seasonal thermal constraints on above-ground activity and can pressure species to remain within refuges for extended periods of time (Webb et al., 2005; Pereira et al., 2019; Ivey et al., 2020). Refuge selection is therefore likely intentionally oriented towards sites that provide appropriate thermal conditions, allowing individuals to maintain body temperatures within their preferred range (Huey, 1991; Kearney and Predavec, 2000; Piantoni et al., 2016; Thompson et al., 2018).

Time spent within refuge sites is influenced by ecological and physiological processes such as predator avoidance, foraging, reproduction and thermoregulation. The time spent foraging is influenced by the efficiency of the foraging animal (MacArthur and Pianka, 1966). Similarly, refuge sites that offer higher thermal quality may be used for a longer duration (Martin and Lopez, 1999b; Cooper and Wilson, 2008; Andersson et al., 2010) and individuals that perceive an increased risk of predation may occupy a refuge site for a longer period of time (Martin and Lopez, 1999b).

Tradeoffs can occur among factors that affect the duration of time spent within refuge. Individuals in refuge may experience a fitness cost of lost foraging and mating opportunities while using a refuge site (Reaney 2007; Martin et al., 2008), and optimality models have been created to predict when optimal emergence time occurs (Sih 1992; Cooper and Fredrick, 2007). In refuge sites that have poor thermal quality, an individual may risk reduced physiological capabilities, hypothermia or hyperthermia, and the duration of occupancy may be reduced

despite a high risk outside of the shelter (Martin and Lopez, 1999a; Martin 2001; Martin and Lopez, 2001; Cooper and Wilson, 2008). Conversely, tradeoffs are reduced when refuge sites provide higher thermal quality or thermal stability (Becker and Brown, 2016) and refuges tend to be used for longer time periods (Martín and Lopez, 1999b; Martín and Lopez, 2001; Andersson et al., 2010).

Thermal quality of refuges may also be influenced by drastic daily or annual thermal fluctuations, which can bring about a temporal shift in refuge selection (Christian et al., 1984; Peterson, 1987; Kearney, 2002; Stelateli et al., 2018). Deeper refuges maintain a more stable microclimate and may be preferred during periods which regularly experience suboptimal above-ground temperatures due to reduced exposure to thermal extremes within the refuge (Scheffers et al., 2014). In habitats that experience significant thermal fluctuations, typically higher latitudes and elevations, thermoregulatory behaviors are important as temperatures may regularly be outside of the preferred temperature range (Piantoni et al., 2016).

Here, we investigate the thermal regimes of refuge sites selected by the Gila monster (*Heloderma suspectum*), a reclusive lizard endemic to deserts of the southwestern United States and northwestern Mexico (Bogert and Martin del Campo, 1956). Gila monsters have a relatively low preferred body temperature range compared to most desert lizards (Lowe et al., 1986; Firth et al., 1989; Gienger et al., 2013; Ivey et al., 2020), have activity patterns that are strongly constrained by the thermal environment (Gienger, 2009), and experience a significant increase in evaporative water loss when exposed to temperatures over 35°C (DeNardo et al., 2004). Gila monsters spend approximately 95% of time in below-ground shelters, including natural crevices under rocks, rodent burrows, and tortoise dens, which provide a thermal buffer from extreme above-ground temperatures (Beck, 1990; Gienger, 2003). Although seemingly abundant on the

landscape, refuges used by Gila monsters (burrows, crevices, caves, etc.) have somewhat predictable physical structure, and specific sites are often reused year after year (Beck, 1990; Gienger, 2003; Beck and Jennings, 2003). Since above-ground thermal regimes are unsuitable for activity throughout much of the spring and summer activity season (Gienger, 2009), and because their preferred body temperatures are relatively low (Gienger et al., 2013), we expect that refuge selection is thermally-mediated in Gila monsters and that refuge site selection should be driven by thermal quality of available refuges. We predict that sites used by Gila monsters provide more opportunities for time within the preferred body temperature range than similar unused shelters and will deviate less from that range. Selected refuges should also have more thermal stability (predictability) than sites not used and therefore should provide a buffer from lethal temperatures. Finally, because Gila monsters might be expected to utilize high quality thermal refuge sites for as long as possible when temperatures permit, we predict that Gila monsters should occupy shelters with higher thermal quality longer than shelters with lower thermal quality.

## **Methods:**

### *Study Site*

The study was conducted approximately 10 km west of Las Vegas, Nevada in the Mojave Desert. The site is primarily Aztec Sandstone and limestone (Lei, 2003), dominated by desert scrub vegetation including native catclaw (*Acacia greggi*), yuccas (*Yucca baccata*, *Yucca brevifolia* and *Yucca schidigera*), and cacti (many species of *Opuntia*, *Echinocactus*, *Ferocactus* and *Cylindropuntia*), as well as invasive cheat grass (*Bromus tectorum*) and red brome (*Bromus rubens*) (Brown, 1994). Mean precipitation from April through July is 4 cm, and the mean

humidity of each month ranging from 15-25% (2011-2020). The study was conducted from April through July 2020, during the active season for Gila monsters, which is when above-ground temperatures are permissible for activity (Gienger 2009), adult males undergo spermiogenesis and adult females are reproductively receptive (Goldberg and Lowe, 1997), and when prey availability is highest (Beck 2005).

### *Experimental Design*

Captured adult and subadult Gila monsters were surgically implanted with a radio transmitter and were radio-tracked five to seven times a week using a radio antenna (Telonics RA-23) and a handheld radio receiver (Advanced Telemetry Systems, Inc. Model R140). When lizards were tracked to an underground shelter, the site was georeferenced and temporarily marked with an identification number using chalk on a rock placed near the opening of the shelter. We measured the physical attributes of shelters using procedures similar to those of Beck and Jennings (2003). We considered refuge sites used by Gila monsters as “actual shelters” and unlike the study by Beck and Jennings, the actual shelters in our study were intentionally paired with nearby shelters that have similar physical shelter characteristics to the actual shelter, which may influence the microhabitat within the shelter. Because we did not know whether paired sites were ever used by the lizards, the shelter was considered a “potential shelter”. We selected potential shelter sites that were within 50 m of the actual site and were of similar type (sandstone crevice, rocky slope, rodent burrow, or tortoise den), entrance height and width, crevice depth, rockiness of the ceiling and floor, and directional azimuth of the entrance. Rockiness was measured on a scale of 1 to 5 where 1 indicates sand and 5 indicates solid rock. A third “random shelter” site was also matched with each pair. Random shelters were shelters that were large

enough to potentially be used by a Gila monster and would permit underground refuge, although we did not attempt to match the physical shelter attributes of the actual shelters. Random shelters were not used in the Beck and Jennings (2003) study. If shelters chosen by Gila monsters did not differ in thermal quality from random shelters, it would indicate that any refuge site, regardless of physical shelter attributes, would offer similar thermal properties and that shelter selection is not thermally-mediated.

After the lizard left the actual shelter, we placed a HOBO datalogger (Onset® UA-001-64) in each trio of actual, potential, and random shelters. Beck and Jennings (2003) found that the temperature of the shelter while being occupied by a Gila monster and after the Gila monster had left did not differ. Therefore, we can assume that the thermal regimes after the lizard had left would be similar to when the lizard had occupied the shelter. Dataloggers for actual and potential shelters were placed at the same depth, typically as deep as the Gila monsters could be sheltered. Random shelters had dataloggers placed at haphazard depths within the shelter, usually close to the deepest area of the shelter. Temperatures were recorded every ten minutes for 72 hours, and loggers were removed, and offloaded using HOBOWare software.

### *Thermal Quality*

We compared the overall (72 h) mean temperatures of shelters among treatments and used the framework of Hertz et al. (1993) to calculate measures of biologically relevant thermal regimes for ectothermic animals. By using biologically informative thermal indices, we can analyze thermal regimes using metrics that have physiological importance, and we can measure nuance which may be lost when only comparing mean overall temperatures. We measured the amount of time (h/day) and proportion of time (out of 72 h) that actual, potential, and random

shelters remained within the preferred thermoregulatory set-point range for Gila monsters (Gienger et al., 2013). The set-point range ( $T_{set}$ ) is determined in a laboratory thermal gradient where it is assumed there are no ecological constraints or costs of thermoregulation, and animals can freely maintain their preferred body temperature ( $T_b$ ). The  $T_{set}$  parameter can be measured as the central 50% or 68% (one standard deviation) of all temperatures recorded (Dewitt and Friedman, 1979; Hertz et al., 1993). The set-point range for Gila monsters is 23.6-27.1°C (Gienger et al., 2013), measured as the central 50% of body temperatures observed.

Also following Hertz et al. (1993), we calculated  $d_e$  for each recorded temperature as the absolute deviation between  $T_{set}$  and the environmental temperature ( $T_e$ ) within shelters. We used  $\bar{d}_e$  as a summary metric for each shelter. Since  $d_e$  measures the deviation between  $T_{set}$  and  $T_e$ , a lower  $d_e$  indicates higher thermal quality, and a higher  $d_e$  (being farther from the preferred range) indicates lower thermal quality.

### *Thermal Stability*

To gage the stability of temperatures in each shelter, we calculated the standard deviation of the overall mean for each shelter. Lower standard deviations indicate more stable temperatures within shelters, whereas higher standard deviations would indicate more variable temperatures. Thermal stability alone may not be informative but can be used in conjunction with thermal quality metrics to gage thermal suitability. Standard deviation was analyzed as a response variable against the shelter type (actual, potential and random shelters).

### Statistical Analysis

Statistics were calculated using R 3.6.2 (R Core Team, 2019). Most of the physical shelter attributes (shelter entrance height, width, depth, logger depth, and rockiness of the floor and roof) were each compared among shelter types using a non-parametric Kruskal-Wallis H-test. Parametric tests could not be used since residuals of a linear model were not normally distributed. For evaluating the directional azimuth of the shelter opening, we used a high-concentration ANOVA for circular data using the *Directional* package (v4.4; Tsagris et al., 2020).

We used a linear mixed effects model for comparison of thermal indices (mean temperature,  $T_{set}$ ,  $\bar{d}_e$ , and standard deviation) among the actual, potential, and random shelters and the packages *lme4* (v1.1-21; Bates et al., 2015) and *lmerTest* (v3.1-3; Kuznetsova et al., 2017). To meet the assumption of normally distributed residuals in thermal quality analyses, the amount of time spent within  $T_{set}$  was square root transformed and standard deviation, duration of occupancy, and the observed number of lizards using a shelter were log transformed. We modeled individual lizard ID and shelter ID as random effects; month was considered a fixed effect to examine temporal effects across increasingly warm periods of the April-July activity season. We did not examine differences between sex, age, size or reproductive condition because we do not know if preferred temperatures differ among the different classes of those variables. We followed comparisons of main effects with a Tukey HSD test for pairwise comparisons.

## Results:

### *Shelters*

We tracked 14 lizards to 234 shelters from April through July 2020 and recorded temperatures for 48 groups of actual, potential, and random shelters. We found no differences in the physical attributes (height, width, depth, roof, depth, directional azimuth and logger depth) between actual and potential shelters ( $p > 0.05$  for all post-hoc comparisons; Table 1). Random shelters were similar to actual and potential shelters in directional azimuth ( $\kappa = 1.81$ ,  $p = 0.250$ ) and roof structure ( $\chi^2(2) < 0.01$ ,  $p = 1.000$ ). However, random shelters differed from the other groups in height ( $\chi^2(2) = 8.53$ ,  $p = 0.014$ ), width ( $\chi^2(2) = 11.71$ ,  $p = 0.003$ ), depth ( $\chi^2(2) = 19.42$ ,  $p < 0.001$ ), floor rockiness ( $\chi^2(2) = 23.28$ ,  $p < 0.001$ ) and depth at which the data logger was inserted ( $\chi^2(2) = 21.84$ ,  $p < 0.001$ ).

### *Thermal Quality*

Mean overall shelter temperatures were nearly identical among treatments (actual shelters =  $28.3 \pm 3.9^\circ\text{C}$ , potential shelters =  $28.6 \pm 5.0^\circ\text{C}$ , random shelters =  $28.4 \pm 5.0^\circ\text{C}$ ,  $F_{2,94} = 0.56$ ,  $p = 0.575$ , Figure 1). We found that mean temperatures did not differ among shelter types by month ( $F_{2,88} = 2.27$ ,  $p = 0.109$ ; Figure 2); however, there was an interaction between month and shelter type ( $F_{6,88} = 4.32$ ,  $p < 0.001$ ). In July, Gila monsters selected shelters that were cooler than either potential or random shelter types (Figure 2). Selected shelters in July were  $32.0 \pm 1.8^\circ\text{C}$ , while potential and random shelters had mean overall temperatures of  $34.6 \pm 1.0^\circ\text{C}$  and  $34.2 \pm 1.5^\circ\text{C}$ , respectively (pairwise comparisons were  $p < 0.001$ , and  $p = 0.004$ , respectively). We found no difference between the mean temperatures of potential and random shelters ( $p = 0.775$ ). In April, May, and June we found no differences in mean temperatures within months among shelter types ( $p > 0.11$  for all other pairwise comparisons).



Interestingly, random shelters had the most time within  $T_{set}$ , with an average of 21.3% of the time spent within that range, while actual shelters averaged 19.2% of the time within  $T_{set}$ , and potential shelters had 16.0% of the time within  $T_{set}$  ( $F_{2,94} = 3.46$ ,  $p = 0.035$ ). Random shelters set-point range temperatures longer than potential shelters ( $p = 0.027$ ), although we found no difference between actual and potential shelters ( $p = 0.453$ ) or actual and random shelters ( $p = 0.333$ ). Time within  $T_{set}$  showed no overall difference among shelter types by month ( $F_{2,88} = 2.65$ ,  $p = 0.076$ ). For all shelter types, May had the highest proportion of time within  $T_{set}$  (Figure 3) with an average of 37.8% of the time within  $T_{set}$  across all three treatments. During June and July, actual shelters were never within  $T_{set}$ , while potential and random shelters had a diminutive amount of time within that range. Pairwise comparisons showed a difference between actual and potential shelters in the month of April ( $p = 0.011$ ; Figure 3), where actual shelters had  $5.8 \pm 4.7$  hours per day within  $T_{set}$ , while potential shelters had  $3.3 \pm 3.9$  hours per day within  $T_{set}$  ( $n = 17$ ). Random shelters, which had  $6.5 \pm 6.0$  hours per day within  $T_{set}$ , also differed from potential shelters ( $p = 0.005$ ), but not from actual shelters ( $p = 0.969$ ). There were no other significant differences in the remaining post-hoc comparisons ( $p > 0.05$ ).

Over the course of the activity season, actual shelters had the highest overall thermal quality (lowest deviation from  $T_{set}$ ) with a  $\bar{d}_e$  of  $2.84 \pm 1.99^\circ\text{C}$ . Potential shelters and random shelters had a  $\bar{d}_e$  of  $3.78 \pm 2.55^\circ\text{C}$  and  $3.61 \pm 2.76^\circ\text{C}$ , respectively ( $F_{2,94} = 7.96$ ,  $p < 0.001$ ). Post-hoc comparisons found thermal quality was higher in actual shelters than both potential shelters ( $p < 0.001$ ) and random shelters ( $p = 0.008$ ). The  $\bar{d}_e$  among the shelter types varied by month ( $F_{2,88} = 19.08$ ,  $p < 0.001$ ; Figure 4); in June, actual shelters had higher thermal quality than random shelters, and in July, actual shelters had higher thermal quality than both other shelter types (Figure 5). In June, the  $\bar{d}_e$  for actual shelters was  $3.0 \pm 1.2^\circ\text{C}$ , compared to  $4.6 \pm 2.4^\circ\text{C}$  for

random shelters ( $p = 0.009$ ). Potential shelters had  $\bar{d}_e$  measured at  $4.1 \pm 2.1^\circ\text{C}$ , which was not different when compared to shelters selected by Gila monsters ( $p = 0.085$ ) or random shelters ( $p = 0.649$ ). In July, actual shelters had  $\bar{d}_e$  of  $4.9 \pm 1.8^\circ\text{C}$ , compared to  $7.5 \pm 1.0^\circ\text{C}$  for potential shelters ( $p < 0.001$ ) and  $7.1 \pm 1.5^\circ\text{C}$  for random shelters ( $p < 0.001$ ). All other post-hoc comparisons found no within-month differences among the thermal quality of shelter types ( $p > 0.47$  for all other pairwise comparisons).

### *Thermal Stability*

Throughout the course of our study, actual shelters had a mean standard deviation of the overall mean temperature of  $1.38^\circ\text{C}$ , compared to  $1.76^\circ\text{C}$  for potential shelters, and  $2.21^\circ\text{C}$  for random shelters ( $F_{2,94} = 10.83$ ;  $p < 0.001$ ; Figure 6). Actual shelters had smaller temperature variations than either potential shelters ( $p = 0.020$ ) or random shelters ( $p < 0.001$ ). Temperature variation in shelters chosen by Gila monsters decreased each month from April to July, but this pattern was not reflected in the other shelter types (Figure 7). Standard deviation of the overall mean temperature among shelter types differed by month ( $F_{2,88} = 17.24$ ,  $p < 0.001$ ; Figure 6); in June, actual shelters had lower thermal fluctuations than random shelters, and in July, actual shelters experienced lower thermal fluctuations than both other types. In June, we measured the standard deviation of the overall mean temperature for actual shelters to be  $0.68^\circ\text{C}$  and the random shelter to be  $1.91^\circ\text{C}$  ( $p = 0.014$ ). In July, mean standard deviations of the overall mean temperature were  $0.43^\circ\text{C}$  for actual shelters,  $1.49^\circ\text{C}$  for potential shelters ( $p < 0.001$ ) and  $1.93^\circ\text{C}$  for random shelters ( $p < 0.001$ ). We found no other monthly difference in the thermal variation among shelter types ( $p > 0.08$  for all other pairwise comparisons within months).

Shelters that are more thermally stable offer more predictable thermal regimes. By selecting for sites that are thermally predictable, Gila monsters can avoid refuges with temperatures that are excessively high and potentially lethal. Bogert and Martin del Campo (1956) noted that the critical thermal maximum ( $CT_{max}$ ) for Gila monsters is 42.5°C, an temperature can lead to partial paralysis in Gila monsters. In our study, sites selected by Gila monsters in our study never had temperatures surpass 40°C (Figure 8). By comparison, over the course of the activity season, potential shelters and random shelters averaged 0.09 and 0.01 h/day above  $CT_{max}$ , respectively (Figure 9).

### *Occupancy and Usage*

Of the 48 shelters measured, we observed eight used for more than seven days, all of which were in early April before the peak of the activity season. In May and July, the longest shelter occupancy was six days; in June, the longest was four days (Figure 10a). We found overall differences in the duration of occupancy by month ( $F_{2,37} = 4.24$ ,  $p = 0.011$ ). Post-hoc differences indicated that duration of occupancy was higher in April than the months of May ( $p = 0.019$ ) and June ( $p = 0.042$ ). We found no other differences in post-hoc comparisons ( $p > 0.50$  for all comparisons). We observed two shelters used by four lizards, four of the shelters used by three lizards, and eight of the shelters were observed to be used by two Gila monsters.

Thermal quality of shelters did not influence the duration of occupancy. There was no effect of time spent within  $T_{set}$  ( $t_{45} = 0.834$ ,  $p = 0.409$ ; Figure 10b), or  $\bar{d}_e$  of a shelter ( $t_{45} = 0.110$ ,  $p = 0.913$ ; Figure 10c) on occupancy duration. We found no effect of thermal quality by month on the duration of occupancy in shelters ( $p > 0.97$  for all comparisons).

In addition, thermal quality did not influence the number of lizards that used a shelter. There was no effect of the amount of time shelters were within  $T_{set}$  ( $t_{45} = -0.785$ ;  $p = 0.437$ ), or  $\bar{d}_e$  of a shelter ( $t_{45} = 0.370$ ;  $p = 0.713$ ) on the total number of lizards observed occupying the shelter. We also found no effect of thermal quality by month on the number of observed lizards occupying shelters ( $p > 0.98$  for all comparisons).

It should be noted that in the months of June and July no actual shelters were ever within  $T_{set}$ , therefore both months were excluded from monthly analyses when  $T_{set}$  was measured as the predictor variable.

## **Discussion:**

Overall, we found mixed support for the hypothesis that shelter selection in Gila monsters is thermally-mediated, albeit in ways that change across the activity season as the thermal environment itself changes. We did not find differences in overall mean temperatures among shelter types, results that similarly reflect the findings of Beck and Jennings (2003), who report nearly identical mean temperatures between actual and potential shelters. When we examined the mean temperatures for each shelter type by month, we found that during the hottest period of the year, July, Gila monsters selected refuges that were 2°C lower than both potential shelters and randomly available shelters. Similarly, Webb et al. (2005) found that refuge sites for Broad-headed Snakes (*Hoplocephalus bungaroides*) had mean temperatures that were often similar between sites with and without vegetative canopy cover, despite clear differences in other thermal properties (minimum, maximum, nighttime and midday temperatures). In addition, a study examining the overwintering sites of predatory arthropods found that in the second winter of ridge establishment, densities of arthropods were higher in vegetation that had less variable

thermal regimes despite no differences in mean overall temperatures above or below the substrate (Thomas et al., 1991). Together this suggests that mean temperature alone may not always be an informative metric to quantify aspects of thermal refuges for organisms in the field, as it lacks context for the biologically nuanced ways in which organisms potentially gage thermal suitability.

Similarly, we found no overall difference between selected shelters and other shelter types in the duration that temperatures remained within the preferred temperature range ( $T_{set}$ ) over the course of the activity season, although random shelters did retain  $T_{set}$  temperatures for a longer duration than potential shelters. However, we found a temporal shift in selection of shelters that hold  $T_{set}$  for a longer period of time. Early in the activity season (April), Gila monsters selected shelters that had more time in  $T_{set}$  when compared to potential shelters, although chosen refuge sites did not differ from randomly available sites. During this month, above-ground temperatures were typically cooler than preferred temperatures for Gila monsters, and the lizards had relatively less movements than compared to the warmer months in the activity season. Before emergence from hibernation, and throughout early spring, Gila monsters thermoregulate by basking at the opening of shelters, routinely achieving body temperatures within  $T_{set}$  despite much lower environmental temperatures (Beck, 1990). In our study, shelters that were selected maintained temperatures that would provide more opportunities for thermoregulation than shelters with similar physical shelter attributes during early spring. We also found that shelters used by Gila monsters had the highest thermal quality among the three shelter types, with a lower deviation from  $T_{set}$  ( $\bar{d}_e$ ) across the activity season. The effect of thermal quality was especially pronounced in June and July, when above-ground temperatures were highest, and mean hourly temperatures within all shelter types were always outside of  $T_{set}$ .

For lizards that live in extreme thermal environments, it is not uncommon for species to be subjected to environmental temperatures outside of their set-point range, and to choose shelters with higher thermal quality. Rock lizards (*Iberolacerta cyreni*) in the Sierra de Guadarrama mountain ranges utilize mixed shrub and rock habitats which have higher thermal quality (lower  $\bar{d}_e$  values) compared to adjacent pine forests where the lizards were absent (Monasterio et al., 2009). Similarly, Aguilar and Cruz (2010) found that Darwin's marked gecko (*Homonota darwini*) were more abundant on a western slope of a hill where the thermal quality of potential refuges was higher than the eastern side of the hill. In addition, selected refuge sites on the western slope had temperatures closer to  $T_{set}$  than unused refuge sites. While we did not look at the body temperatures of Gila monsters for our study, our study implies that Gila monsters would be able to attain more suitable body temperatures at selected refuge sites than other refuges with similar physical shelter attributes, or if shelters were chosen randomly.

We found that thermal stability of refuges appeared to be an important factor in shelter selection, and over the course of the activity season, refuge sites selected by Gila monsters were more thermally stable than other shelter types. Thermal stability was especially pronounced during the warmest months of the activity season (June and July) and potentially reflects the importance of predictability in shelter thermal regimes when above-ground temperatures can be lethal. Thermal stability is observed in the body temperature of Gila monsters, as Beck (1990) found that while in refuge, overall body temperatures typically fluctuated less than 1.0°C daily, presumably reflecting the thermal stability of selected refuges. Similarly, our results indicate low standard deviations in shelters used in June and July (0.68°C and 0.43°C, respectively) despite high daily above-ground temperatures. In June, the mean standard deviation of randomly available shelters was more than double that of actual shelters, and in July was more than three

times greater than actual shelters. Becker and Brown (2016) found that in the summer, two scorpion species (*Vaejovis cashi* and *V. electrum*) occupied larger rocks that offered more stable thermal regimes and lower temperatures than rocks not used as refuge. In addition, Rowland et al. (2017) found that nest boxes deployed as a conservation tool for arboreal marsupials experienced higher temperature fluctuations than natural refuges (tree hollows), often reaching temperatures that could induce heat-stress. The low thermal stability and unsuitable temperatures resulted in low occupancy of the nest boxes. Our results indicate that Gila monsters select sites that are thermally stable, which provide more predictable thermal regimes putatively to avoid potentially lethal temperatures.

We did not find support for our predictions linking thermal quality to the duration of occupancy for Gila monsters within a shelter. We assumed that higher thermal quality would serve as a benefit for Gila monsters and result in increased occupancy of shelters. Previous studies have found that when wall lizards (*Podarcis muralis*) used refuges that provided preferred temperatures, duration of occupancy was increased (Martín and Lopez, 1999b). However, our study occurred during the duration of the activity season for Gila monsters, and longer duration within shelters during this period may present a tradeoff in lost foraging and mating opportunities. Similarly, a study observing the tradeoffs of refuge use in the Iberian rock lizard (*Lacerta monticola*) found that when foraging opportunities increased, *L. monticola* subsequently reduced the duration of occupancy within refuge sites (Martín et al., 2008).

As global temperatures continue to increase due to climate change, an understanding of the role of thermally-mediated refuge selection and occupancy in selected refuge sites is increasingly important (Kearney et al., 2009; Scheffers et al., 2014; Moore et al., 2018). Our study suggests that refuge site selection in Gila monsters is thermally-mediated during the

activity season. Selected shelters early in the spring maintained preferred temperatures more than in comparison to potential shelters that were not used by Gila monsters. In late spring, Gila monsters were more active when above-ground temperatures were optimal and did not select shelters based on thermal properties. Later in the activity season, when ambient temperatures increased to stressful and potentially lethal temperatures, Gila monsters selected shelters that were more thermally stable and deviated less from the preferred range than compared to those that were less stable and had higher temperature fluctuations.



Table 1. Means and standard deviations for shelter attributes measured for each actual, potential, and random shelters (n=48 for each). P-values for height, width, logger depth, depth, roof and floor are from a Kruskal-Wallis H-Test, and the p-value for azimuth is from a high-concentration ANOVA for circular data. Superscripts indicate post-hoc differences using a Dunn's Test. Shelter types with the same superscript letter are not significantly different from one another.

Attributes	Actual	Potential	Random	P-value
Height (cm)	11.6 ± 6.7 <sup>A</sup>	10.8 ± 4.4 <sup>A</sup>	15.7 ± 8.9 <sup>B</sup>	0.014
Width (cm)	26.8 ± 19.0 <sup>A</sup>	26.9 ± 17.4 <sup>A</sup>	39.6 ± 29.4 <sup>B</sup>	0.003
Depth (cm)	80.5 ± 33.9 <sup>A</sup>	75.8 ± 29.7 <sup>A</sup>	56.1 ± 27.1 <sup>B</sup>	0.000
Roof	4.9 ± 0.6 <sup>A</sup>	4.9 ± 0.6 <sup>A</sup>	4.9 ± 0.5 <sup>A</sup>	1.000
Floor	2.0 ± 1.0 <sup>A</sup>	2.2 ± 1.0 <sup>A</sup>	3.1 ± 1.2 <sup>B</sup>	0.000
Azimuth (°)	173.5 ± 0.7 <sup>A</sup>	174.6 ± 0.8 <sup>A</sup>	191.0 ± 1.3 <sup>A</sup>	0.250
Logger Depth (cm)	72.7 ± 29.4 <sup>A</sup>	69.4 ± 28.3 <sup>A</sup>	48.5 ± 22.5 <sup>B</sup>	0.000

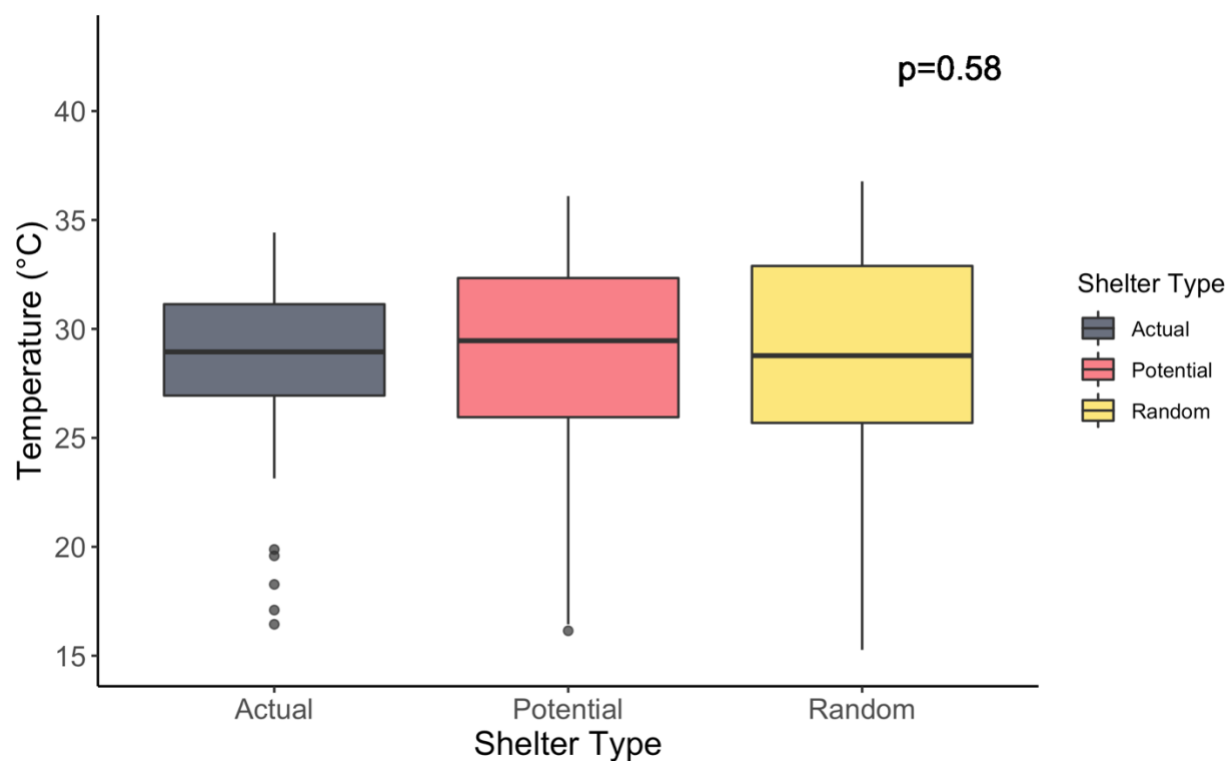


Figure 1. Mean temperature by shelter type (n=48 for each) from April-July 2020. Mean overall temperature did not differ among shelter types. Letters over the box plots indicate post-hoc comparisons using a Tukey's Test. Shelter types with the same letter are not significantly different from one another.

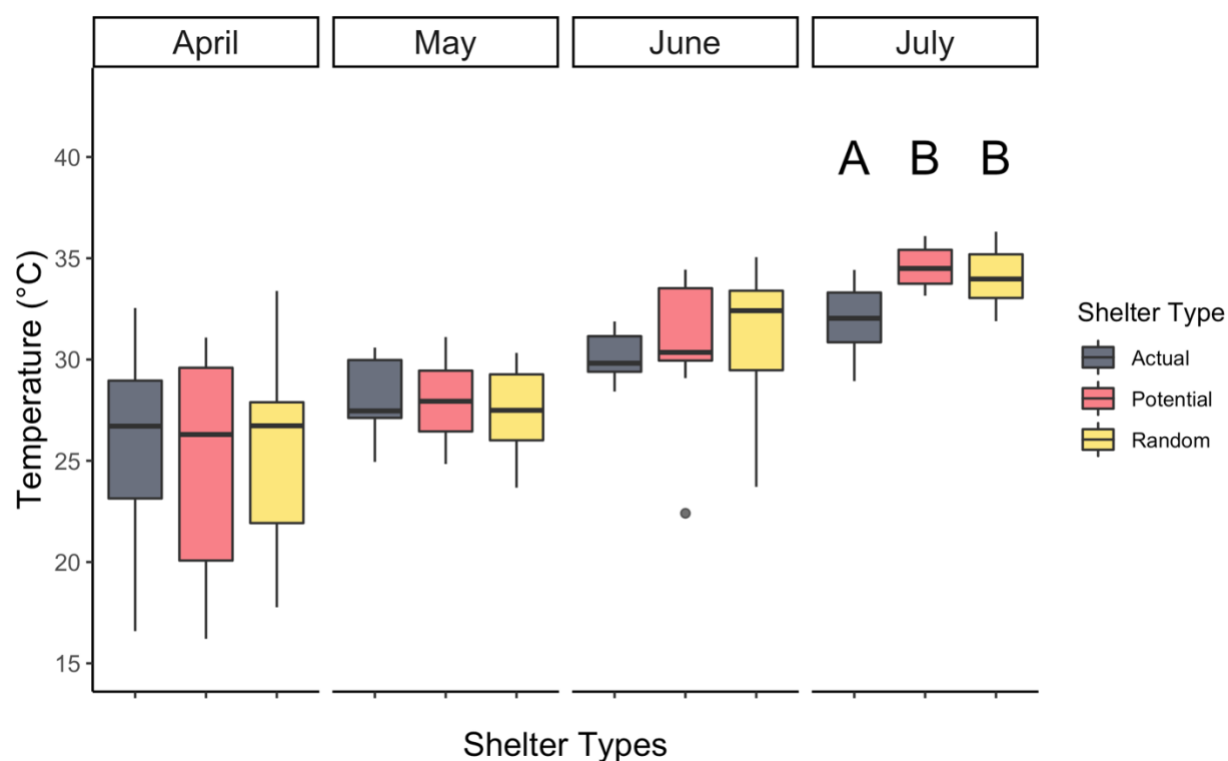


Figure 2. Mean temperature (with standard deviation error bars) for each shelter type by month. (n=17 for April, n=13 for May, n=9 for June, n=9 for July). Letters over the box plots in July indicate within-month post-hoc differences using a Tukey's Test. Shelter types with the same letter are not significantly different from one another; shelter types were not significantly different in April, May, June.

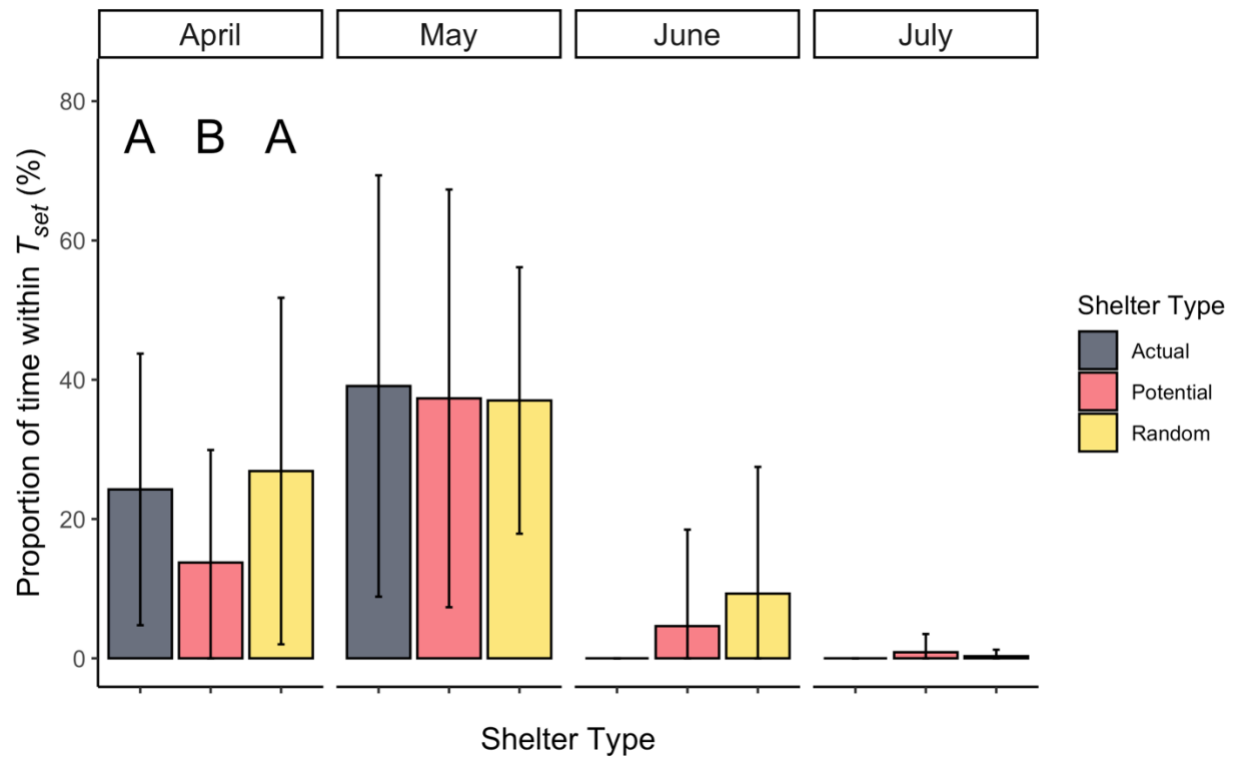


Figure 3. Proportion of time (with standard deviation error bars) within the set-point range ( $T_{set}$ ) by shelter type and by month ( $n=17$  for April,  $n=13$  for May,  $n=9$  for June,  $n=9$  for July). Letters over the box plots in April indicate within-month post-hoc differences using a Tukey's Test. Shelter types with the same letter are not significantly different from one another; shelter types were not significantly different in May, June and July.

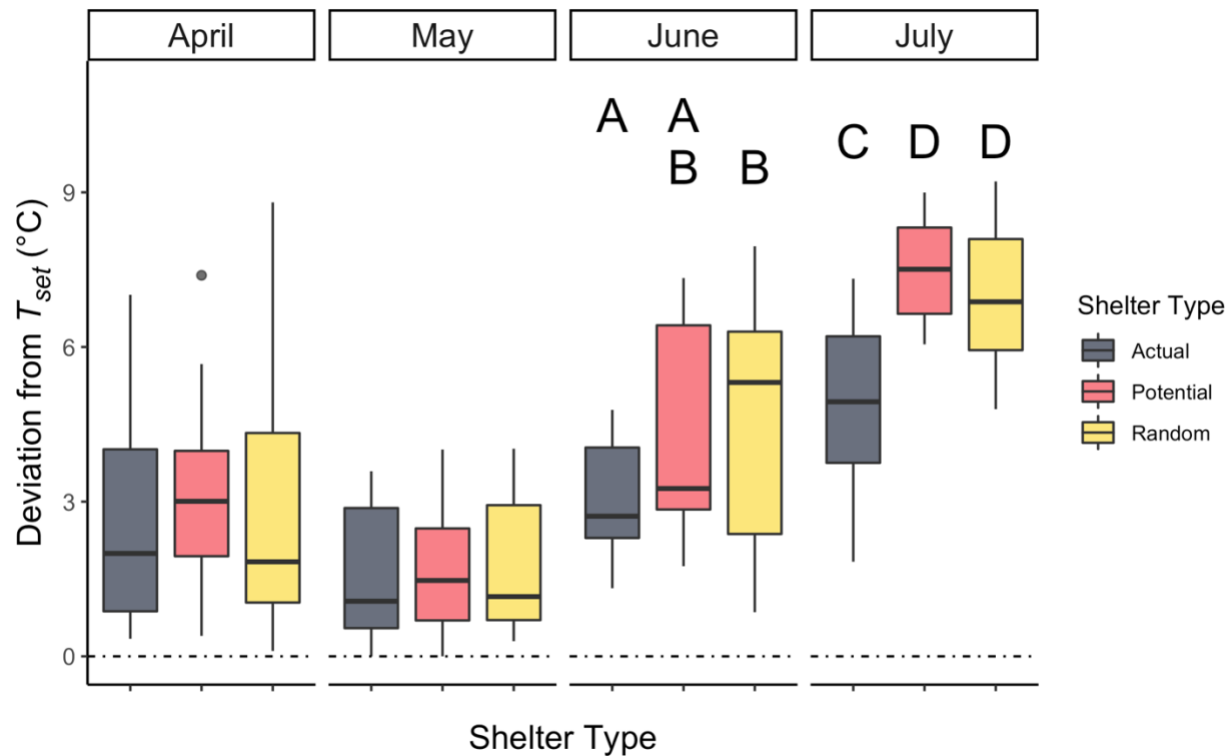


Figure 4. Thermal quality of shelters as measured by mean  $d_e$  (deviation from thermoregulatory set-point range) across months ( $n=17$  for April;  $n=13$  for May;  $n=9$  for June;  $n=9$  for July) with standard deviation error bars. A deviation of  $0^{\circ}\text{C}$  would indicate that the temperature was within the set-point range (noted by dashed line). Letters over the box plots in June and July indicate within-month post-hoc differences using a Tukey's Test. Shelter types with the same letter are not significantly different from one another; shelter types were not significantly different in thermal quality in April or May.

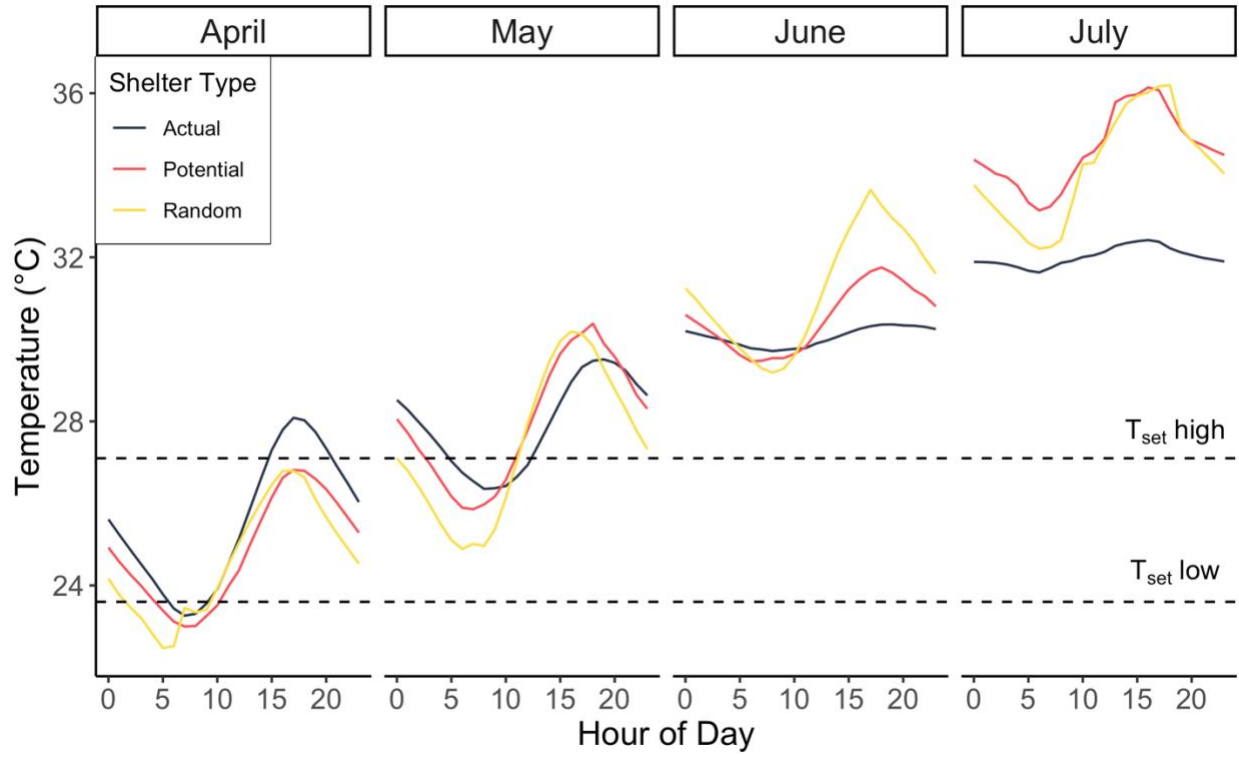


Figure 5. Mean hourly temperature for each shelter type by month and hour of day ( $n=48$ ). The dashed lines indicate the target thermoregulatory range (lower and upper  $T_{set}$ ).

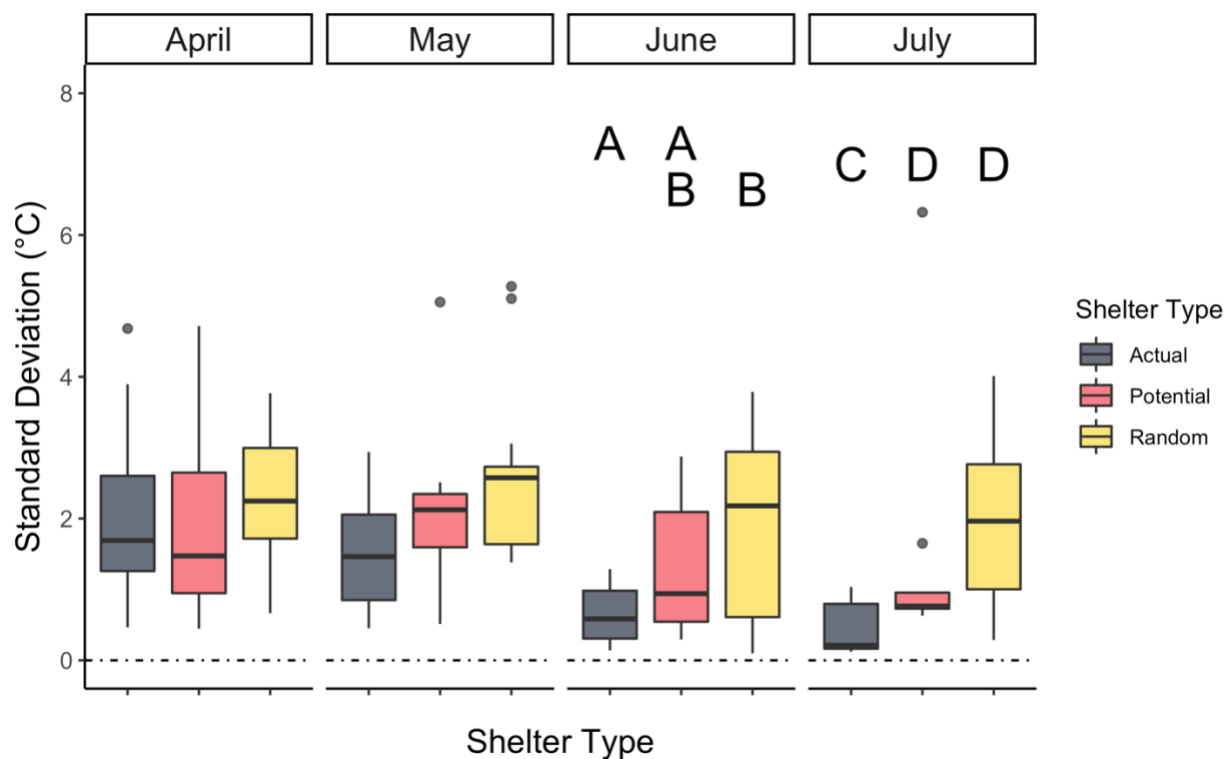


Figure 6. Thermal stability of shelters as measured by standard deviation from the mean temperature for each shelter type across all months ( $n=17$  for April;  $n=13$  for May;  $n=9$  for June;  $n=9$  for July). A deviation of  $0^{\circ}\text{C}$  would indicate that there is no fluctuation of temperature (noted by dashed line). Letters over the box plots in June and July indicate within-month post-hoc differences using a Tukey's Test. Shelter types with the same letter are not significantly different from one another; shelter types were not significantly different in thermal stability in April or May.

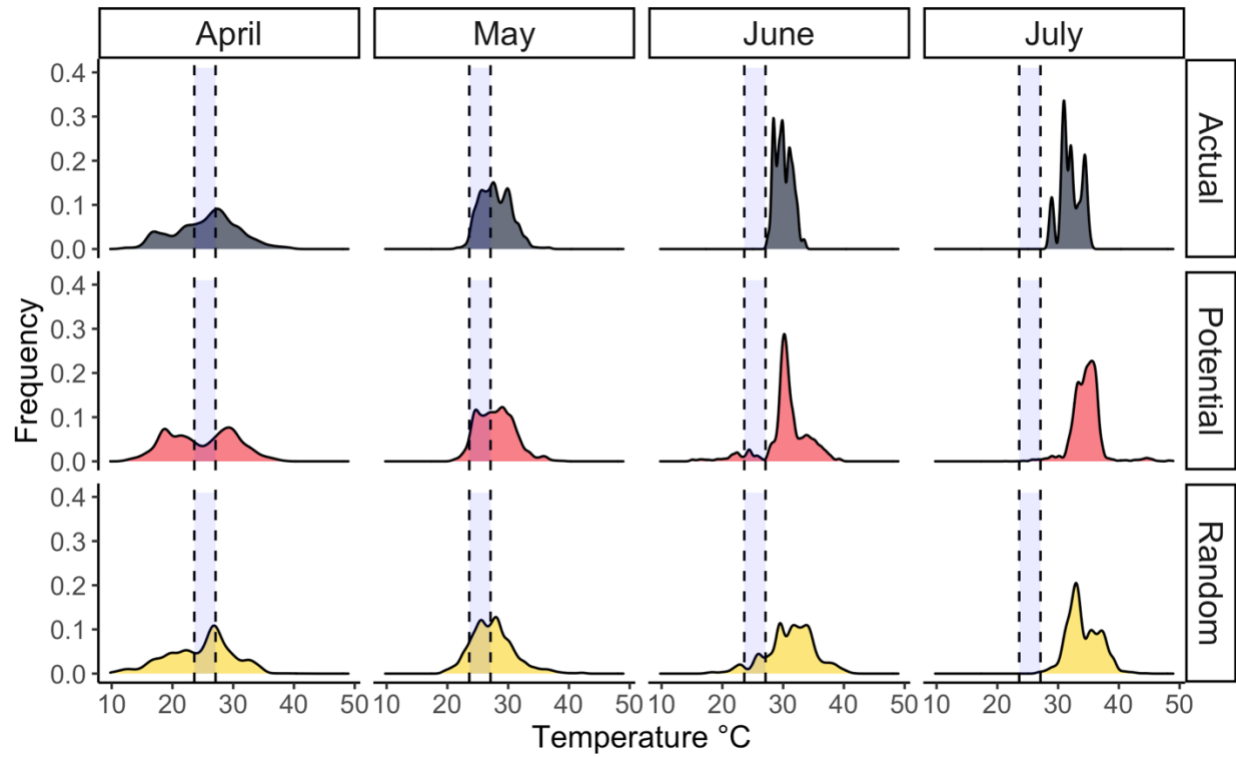


Figure 7. Density plot showing the frequency of temperatures recorded for each shelter type by month. (n=7,361 in April; n=5,629 in May; n=3,897 in June; n=3,897 in July). The shaded blue regions indicate the lower and upper set-point range ( $T_{set}$ ).



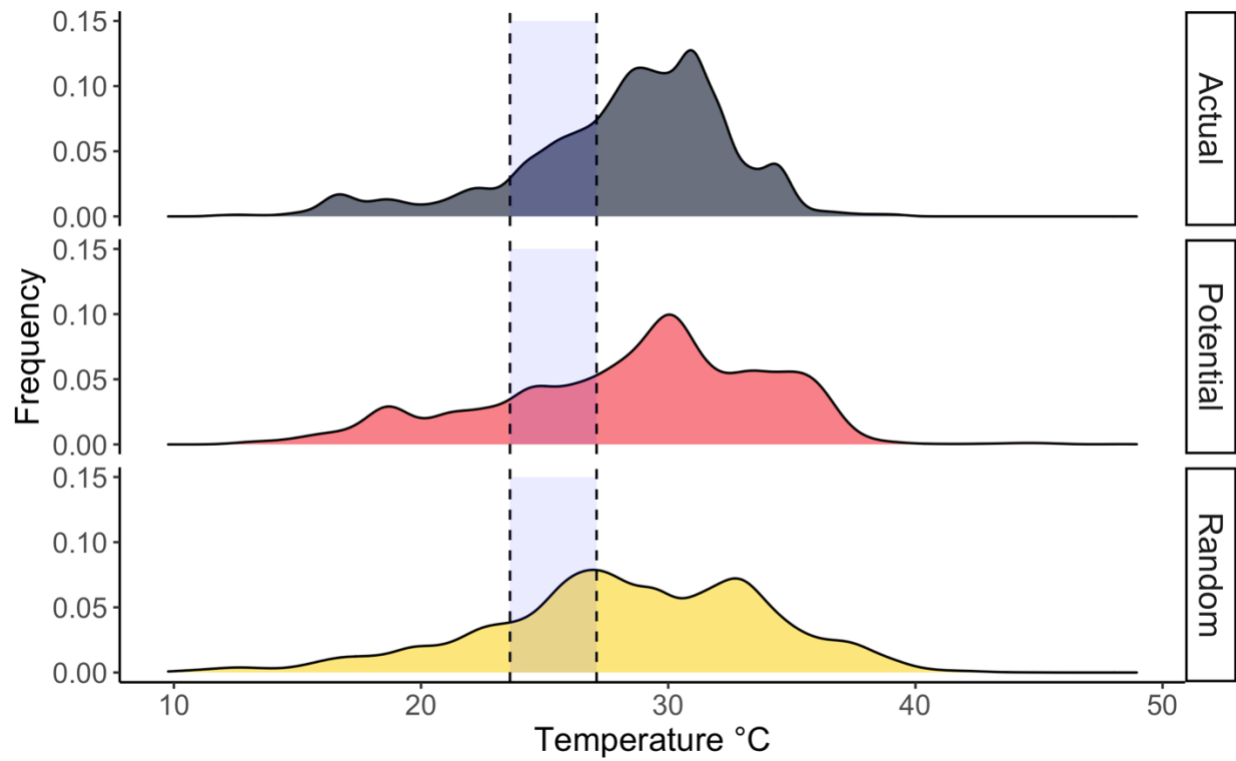


Figure 8. Density plot showing the frequency of all temperatures recorded for each shelter type (n=20,784 for each). The shaded blue regions indicate the lower and upper set-point range ( $T_{set}$ ).

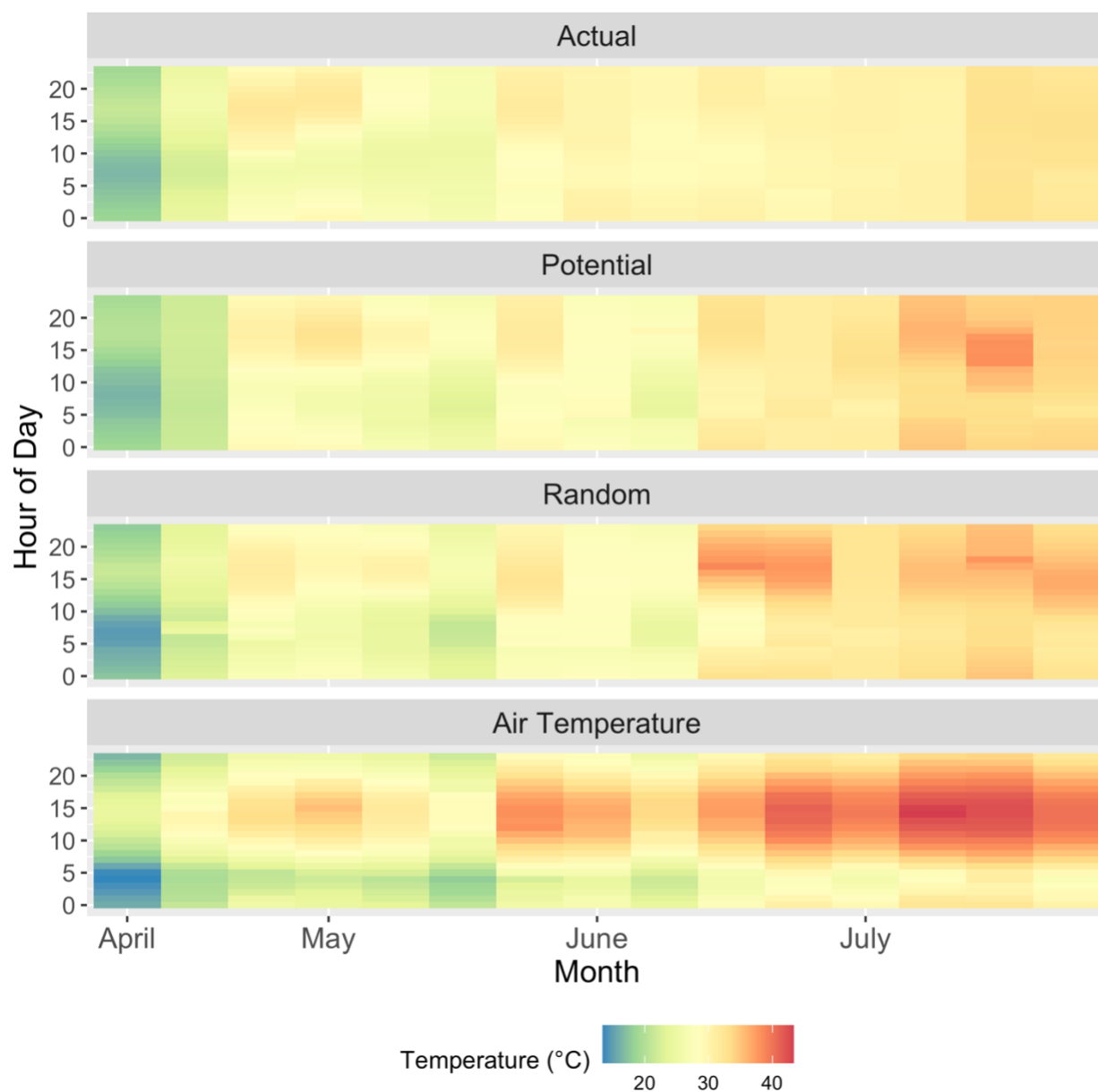


Figure 9. Heat map displaying the hourly means of temperatures within each shelter type and for above-ground air temperatures by week (starting second week of April).

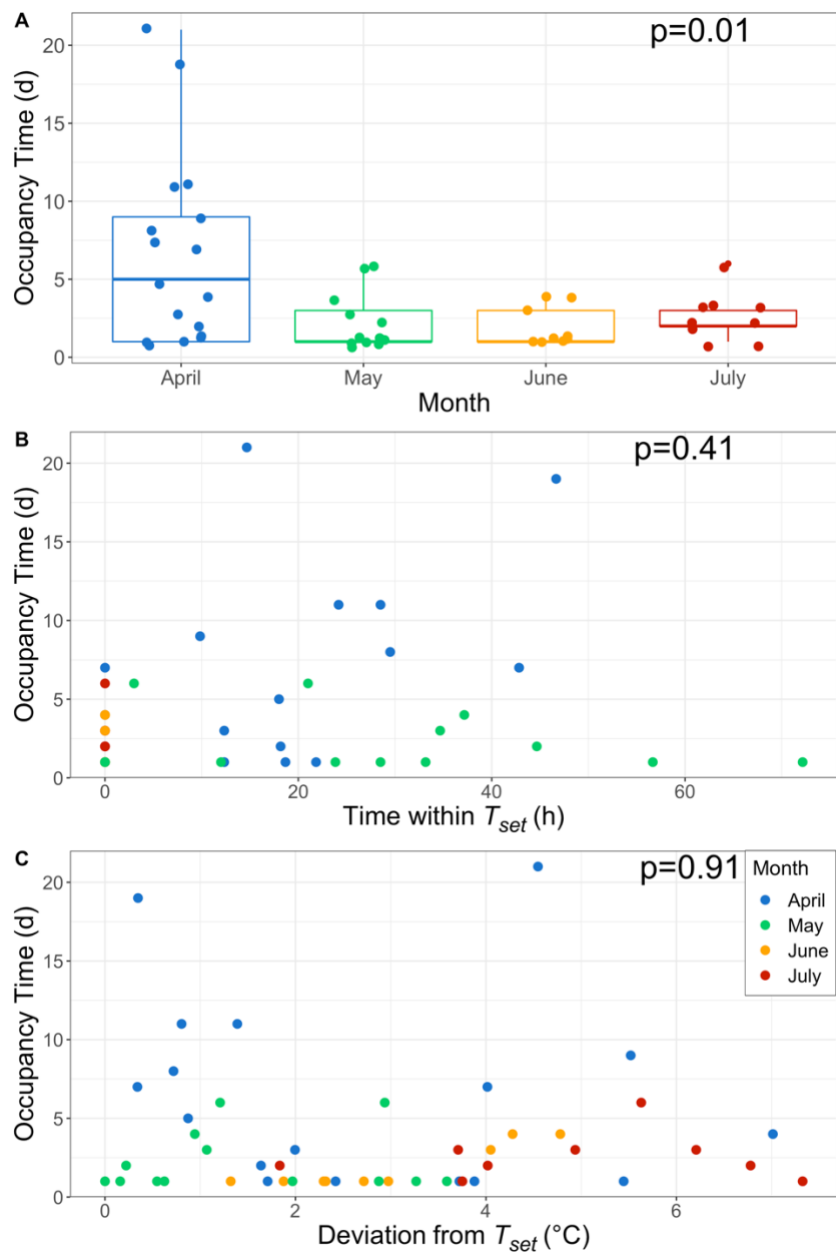


Figure 10. Monthly effect of thermal quality on shelter occupancy. Occupancy duration is plotted A.) against the total hours spent within the set-point range ( $T_{set}$ ), B.) against the average deviation from  $T_{set}$  for each shelter and C.) by month.

## Literature Cited:

- Aguilar, R., Cruz, F.B., 2010. Refuge use in a patagonian nocturnal lizard, *Homonota darwini*: the role of temperature. *J. Herpetol.* 44, 236–241. <https://doi.org/10.1670/08-270.1>
- Andersson, M., Krockenberger, A., Schwarzkopf, L., 2010. Experimental manipulation reveals the importance of refuge habitat temperature selected by lizards. *Austral Ecol.* 35, 294–299.
- Barber, B.J., Crawford, E.C.J., 1977. A stochastic dual limit hypothesis for behavioral thermoregulation in lizards. *Physiol. Zool.* 50, 53–60. <https://doi.org/10.1086/physzool.50.1.30155715>
- Barnes, B.M., Barger, J.L., Seares, J., Tacquard, P.C., Zuercher, G.L., 1996. Overwintering in Yellowjacket queens ( *Vespula vulgaris*) and Green Stinkbugs (*Elasmotethus interstinctus*) in Subarctic Alaska. *Physiol. Zool.* 69, 1469–1480.
- Barton, M., Porter, W., Kearney, M., 2014. Behavioural thermoregulation and the relative roles of convection and radiation in a basking butterfly. *J. Therm. Biol.* 41, 65–71. <https://doi.org/10.1016/j.jtherbio.2014.02.004>
- Bates, D., Maechler, M., Walker, S., 2015. Fitting linear mixed-effects models using {lme4}. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beck, D.D., 1990. Ecology and behavior of the Gila monster in southwestern Utah. *J. Herpetol.* 24, 54–68.
- Beck, D.D., 2005. Biology of Gila monsters and beaded lizards. University of California Press, Berkeley and Los Angeles, California.
- Beck, D.D., Jennings, R.D., 2003. Habitat use by Gila monsters: the importance of shelters. *Herpetol. Monogr.* 17, 111. [https://doi.org/10.1655/0733-1347\(2003\)017\[0111:hubgmt\]2.0.co;2](https://doi.org/10.1655/0733-1347(2003)017[0111:hubgmt]2.0.co;2)
- Becker, J.E., Brown, C.A., 2016. Reliable refuge: two Sky Island scorpion species select larger, thermally stable retreat sites. *PLoS One* 11, Article No.: e0168105. <https://doi.org/10.1371/journal.pone.0168105>
- Berk, M.L., Heath, J.E., 1975. An analysis of behavioral thermoregulation in the lizard, *Dipsosaurus dorsalis*. *J. Therm. Biol.* 1, 15–22. [https://doi.org/10.1016/0306-4565\(75\)90006-6](https://doi.org/10.1016/0306-4565(75)90006-6)
- Bernal, D., Sepulveda, C., Graham, J.B., 2001. Water-tunnel studies of heat balance in swimming mako sharks. *J. Exp. Biol.* 204, 4043–4054.

- Bogert, C.M., 1949. Thermoregulation in reptiles, a factor in evolution. *Evolution* (N. Y). 3, 195–211. <https://doi.org/10.2307/2405558>
- Bogert, C.M., Martin del Campo, R., 1956. The Gila monster and its allies: the relationships, habits, and behavior of the lizards of the family Helodermatidae. *Bull. Am. Museum Nat. Hist.* 109, 1–238.
- Bonnet, X., Fizesan, A., Michel, C.L., 2013. Shelter availability, stress level and digestive performance in the aspic viper. *J. Exp. Biol.* 216, 815–822. <https://doi.org/10.1242/jeb.078501>
- Brown, D.E., 1994. *Biotic Communities: Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City, Utah.
- Christian, K., Tracy, C.R., Porter, W.P., 1983. Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). *Ecology* 64, 463–468. <https://doi.org/10.2307/1939965>
- Christian, K.A., Tracy, C.R., Porter, W.P., 1984. Physiological and ecological consequences of sleeping-site selection by the Galapagos land iguana (*Conolophus pallidus*). *Ecology* 65, 752–758. <https://doi.org/10.2307/1938047>
- Cooper, W.E., Frederick, W.G., 2007. Optimal time to emerge from refuge. *Biol. J. Linn. Soc.* 91, 375–382. <https://doi.org/10.1111/j.1095-8312.2007.00802.x>
- Cooper, W.E., Wilson, D.S., 2008. Thermal cost of refuge use affects refuge entry and hiding time by striped plateau lizards *Sceloporus virgatus*. *Herpetologica* 64, 406–412. <https://doi.org/10.1655/07-083R2.1>
- Cowles, R.B., Bogert, C.M., 1944. A preliminary study of the thermal requirements of desert reptiles. *Bull. Am. Museum Nat. Hist.* 83, 265–296.
- DeNardo, D.F., Zubal, T.E., Hoffman, T.C.M., 2004. Cloacal evaporative cooling: a previously undescribed means of increasing evaporative water loss at higher temperatures in a desert ectotherm, the Gila monster *Heloderma suspectum*. *J. Exp. Biol.* 207, 945–953. <https://doi.org/10.1242/jeb.00861>
- Dewitt, C.B., Friedman, R.M., 1979. Significance of skewness in ectotherm thermoregulation. *Am. Zool.* 19, 195–209. <https://doi.org/10.1093/icb/19.1.195>
- Downes, S., Shine, R., 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. *Anim. Behav.* 55, 1387–1396. <https://doi.org/10.1006/anbe.1997.0705>

- Ebeling, A.W., Hixon, M., 1991. Tropical and temperate reef fishes: comparison of community structures, in: Sale, P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, California, pp. 509–563.
- Eggleston, D.B., Lipcius, R.N., 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology* 73, 992–1011.  
<https://doi.org/10.2307/1940175>
- Firth, B.T., Turner, J.S., Ralph, C.L., 1989. Thermoregulatory behaviour in two species of iguanid lizards (*Crotaphytus collaris* and *Sauromalus obesus*): diel variation and the effect of pinealectomy. *J. Comp. Physiol. B* 159, 13–20.
- Gienger, C.M., 2003. Natural history of the Gila monster in Nevada. University of Nevada-Reno.
- Gienger, C.M., 2009. Foraging, feeding, energetics, and environment: interactions between physiology and ecology of Gila monsters. University of Nevada-Reno.
- Gienger, C.M., Tracy, C.R., Zimmerman, L.C., 2013. Thermal responses to feeding in a secretive and specialized predator (Gila monster, *Heloderma suspectum*). *J. Therm. Biol.* 38, 143–147. <https://doi.org/10.1016/J.JTHERBIO.2012.12.004>
- Goldberg, S.R., Lowe, C.H., 1997. Reproductive cycle of the gila monster, *Heloderma suspectum*, in southern Arizona. *J. Herpetol.* 31, 161–166. <https://doi.org/10.2307/1565350>
- Harlow, P., Grigg, G., 1984. Shivering thermogenesis in a brooding diamond python, *Python spilotes spilotes*. *Copeia* 959–965.
- Heinrich, B., Pantle, C., 1975. Thermoregulation in small flies (*Syrphus* Sp.): basking and shivering. *J. Exp. Biol.* 62, 599–610. <https://doi.org/10.1242/jeb.62.3.599>
- Hertz, P.E., Huey, R.B., Stevenson, R.D., 1993. Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *Am. Nat.* 142, 796–818.  
<https://doi.org/10.1086/285573>
- Holbrook, S.J., Brooks, A.J., Schmitt, R.J., Stewart, H.L., 2008. Effects of sheltering fish on growth of their host corals. *Mar. Biol.* 155, 521–530. <https://doi.org/10.1007/s00227-008-1051-7>
- Holbrook, S.J., Carr, M.H., Schmitt, R.J., Coyer, J.A., 1990. Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. *Bull. Mar. Sci.* 47, 104–114.
- Huey, R.B., 1991. Physiological consequences of habitat selection. *Am. Nat.* 137, S91–S115.  
<https://doi.org/10.1086/285141>

- Huey, R.B., Kingsolver, J.G., 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.* 4, 131–135. [https://doi.org/10.1016/0169-5347\(89\)90211-5](https://doi.org/10.1016/0169-5347(89)90211-5)
- Huey, R.B., Peterson, C.R., Arnold, S.J., Porter, W.P., 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70, 931–944. <https://doi.org/10.2307/1941360>
- Huey, R.B., 1982. Temperature, physiology, and the ecology of reptiles, in: Gans, C., Pough, F.H. (Eds.), *Biology of the Reptilia*. Academic Press, London, pp. 25–91.
- Huey, R.B., Stevenson, R.D., 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* 19, 357–366. <https://doi.org/10.1093/icb/19.1.357>
- Ivey, K.N., Cornwall, M., Crowell, H., Ghazian, N., Nix, E., Owen, M., Zuliani, M., Lortie, C.J., Westphal, M., Taylor, E., 2020. Thermal ecology of the federally endangered blunt-nosed leopard lizard (*Gambelia sila*). *Conserv. Physiol.* 8, coaa014. <https://doi.org/https://doi.org/10.1093/conphys/coaa014>
- Kearney, M., 2002. Hot rocks and much-too-hot rocks: seasonal patterns of retreat-site selection by a nocturnal ectotherm. *J. Therm. Biol.* 27, 205–218. [https://doi.org/10.1016/S0306-4565\(01\)00085-7](https://doi.org/10.1016/S0306-4565(01)00085-7)
- Kearney, M., Predavec, M., 2000. Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology* 81, 2984–2996.
- Kearney, M., Shine, R., Porter, W.P., 2009. The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proc. Natl. Acad. Sci. U. S. A.* 106, 3835–3840. <https://doi.org/10.1073/pnas.0808913106>
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Lei, S.A., 2003. Environmental attributes correlating with density of blackbrush (*Coleogyne ramosissima*) shrubs in the Spring Mountains of southern Nevada. *West. North Am. Nat.* 63, 391–399.
- Lowe, C.H., Schwalbe, C.R., Johnson, T.B., 1986. *The venomous reptiles of Arizona*. Arizona Game and Fish Department, Phoenix, AZ.
- MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *Am. Nat.* 100, 603–609. <https://doi.org/10.1086/282454>
- Martín, J., 2001. When hiding from predators is costly: optimization of refuge use in lizards. *Etologia* 9, 9–12.

- Martín, J., Lopez, P., 2001. Repeated predatory attacks and multiple decisions to come out from a refuge in an alpine lizard. *Behav. Ecol.* 12, 386–389. <https://doi.org/10.1093/beheco/12.4.386>
- Martín, J., Lopez, P., 1999. When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behav. Ecol.* 10, 487–492. <https://doi.org/10.1093/beheco/10.5.487>
- Martín, J., Lopez, P., 1999. An experimental test of the costs of antipredatory refuge use in the wall lizard, *Podarcis muralis*. *Oikos* 84, 499–505.
- Martín, J., Lopez, P., Cooper, W.E., 2008. When to come out from a refuge: balancing predation risk and foraging opportunities in an alpine lizard. *Ethology* 109, 77–87. <https://doi.org/10.1046/j.1439-0310.2003.00855.x>
- Monasterio, C., Salvador, A., Iraeta, P., Diaz, J.A., 2009. The effects of thermal biology and refuge availability on the restricted distribution of an alpine lizard. *J. Biogeogr.* 39, 1673–1684. <https://doi.org/10.1111/j.1365-2699.2009.02113.x>
- Moore, D., Stow, A., Kearney, M.R., 2018. Under the weather?—The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system. *J. Anim. Ecol.* 87, 660–671. <https://doi.org/10.1111/1365-2656.12812>
- Nordberg, E.J., Cobb, V.A., 2017. Body temperatures and winter activity in overwintering timber rattlesnakes (*Crotalus horridus*) in Tennessee, USA. *Herpetol. Conserv. Biol.* 12, 606–615.
- Pereira, J.J., Lopes, E.P., Carretero, M., Vasconcelos, R., 2019. Insular geckos provide experimental evidence on refuge selection priorities by ectotherms. *Behav. Processes* 164, 260–267. <https://doi.org/10.1016/j.beproc.2019.03.008>
- Peterson, C.R., 1987. Daily variation in the body temperatures of free-ranging garter snakes. *Ecology* 68, 160–169.
- Piantoni, C., Navas, C.A., Ibarguengoytia, N.R., 2016. Vulnerability to climate warming of four genera of New World iguanians based on their thermal ecology. *Anim. Conserv.* 19, 391–400. <https://doi.org/10.1111/acv.12255>
- Reaney, L.T., 2007. Foraging and mating opportunities influence refuge use in the fiddler crab, *Uca mjoebergi*. *Anim. Behav.* 73, 711–716. <https://doi.org/10.1016/j.anbehav.2006.05.022>
- Rowland, J.A., Briscoe, N.J., Handasyde, K.A., 2017. Comparing the thermal suitability of nest-boxes and tree-hollows for the conservation-management of arboreal marsupials. *Biol. Conserv.* 209, 341–348. <https://doi.org/10.1016/j.biocon.2017.02.006>



- Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E., Evans, T.A., 2014. Microhabitats reduce animal's exposure to climate extremes. *Glob. Chang. Biol.* 20, 495–503. <https://doi.org/10.1111/gcb.12439>
- Sih, A., 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *Am. Nat.* 139, 1052–1069. <https://doi.org/10.1086/285372>
- Stanton-Jones, W.K., Parusnath, S., Alexander, G.J., 2018. The impact of posture and basking orientation on thermoregulation in the Sungazer (*Smaug giganteus*). *J. Therm. Biol.* 75, 45–53. <https://doi.org/10.1016/j.jtherbio.2018.05.005>
- Stellatelli, O.A., Villalba, A., Block, C., Estela Vega, L., Esteban Dajil, J., Benjamin Cruz, F., 2018. Seasonal shifts in the thermal biology of the lizard *Liolaemus tandiliensis* (Squamata, Liolaemidae). *J. Therm. Biol.* 73, 61–70. <https://doi.org/10.1016/j.jtherbio.2018.02.009>
- Thomas, M.B., Wratten, S.D., Sotherton, N.W., 1991. Creation of “island” habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. *Br. Ecol. Soc.* 38, 906–917.
- Thompson, M.E., Halstead, B.J., Donnelly, M.A., 2018. Thermal quality influences habitat use of two anole species. *J. Therm. Biol.* 75, 54–61. <https://doi.org/https://doi.org/10.1016/j.jtherbio.2018.05.007>
- Tsagris, M., Athineou, G., Sajib, A., Amson, E., Waldstein, M.J., 2020. Directional: Directional Statistics.
- Vasconcelos, R., Santos, X., Carretero, M.A., 2012. High temperatures constrain microhabitat selection and activity patterns of the insular Cape Verde wall gecko. *J. Arid Environ.* 81, 18–25. <https://doi.org/10.1016/j.jaridenv.2012.01.013>
- Vinegar, A., 1968. Metabolism, energetics and thermoregulation during brooding of snakes of the genus *Python* (Reptilia Boidae). University of Rhode Island.
- Wcisel, M., O’Riain, M.J., de Vos, A., Chivell, W., 2015. The role of refugia in reducing predation risk for Cape fur seals by white sharks. *Behav. Ecol. Sociobiol.* 69, 127–138. <https://doi.org/10.1007/s00265-014-1825-5>
- Webb, J.K., Shine, R., Pringle, R.M., 2005. Canopy removal restores habitat quality for an endangered snake in a fire suppressed landscape. *Copeia* 2005, 894–900.
- Webb, J.K., Shine, R., 2000. Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles? *Biol. Conserv.* 92, 93–99. [https://doi.org/10.1016/S0006-3207\(99\)00056-7](https://doi.org/10.1016/S0006-3207(99)00056-7)

Wegner, N.C., Snodgrass, O.E., Dewar, H., Hyde, J.R., 2015. Whole-body endothermy in a mesopelagic fish, the opah, *Lampris guttatus*. *Science* (80-. ). 348, 786–789.  
<https://doi.org/10.1126/science.aaa8902>