



Final Project Report – 2019-AUSTINPEAY-1997B

Gila Monster Spatial Ecology and Habitat Use

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Executive Summary

To better understand threats to persistence of Gila monsters in southern Nevada, we conducted investigations regarding their movement, habitat use, and spatial ecology. The ecology of southern Nevada Gila monsters has historically remained a mystery because of their typically patchy distribution of populations, low population densities, and relatively unknown habitat requirements. We use field surveys, radio telemetry, and measurements of refuge site selection to examine how Gila monsters move across the landscape and select refugia. Data were sourced both from field investigations and from unpublished information; combining contemporary and historical data allowed analyses of up to five continuous years of data from two different populations. Since Gila monsters spend the vast majority of their time underground (>95% in some cases), understanding the environmental influences on movement and refuge site selection should help identify key features of the species habitat requirements.

Introduction

Gila monsters (*Heloderma suspectum*) are among the rarest and most secretive animals in Nevada. As a result, we currently lack basic information to assess species status and how the species will be affected by changes in habitat (i.e. development, degradation, fragmentation) and climate. Gila monsters are known to occupy much of eastern Clark County and southern Lincoln County in Nevada, but due to rarity, our knowledge of the extent of this species is incomplete.

This project focused on determining the multi-scale habitat requirements for Gila monsters in southern Nevada and identify critical habitat resources that can be used in planning efforts for the species.

Methods and Materials

Gila monsters were tracked using standard VHF radio-telemetry methods. Lizards were collected and transported to a laboratory and surgically implanted intracelomically with 15 g radio. Locations of individual lizards were obtained by GPS and coordinates recorded using the Universal Transverse Mercator (UTM) system. For each animal relocation, the date, time of activity (if animal is active), microhabitat, and distance moved from previous fix was recorded. Home range and movement estimates were calculated for each individual to gage cumulative annual spatial habitat use and the potential for dispersal among populations.

Characteristics of refuge sites used by Gila Monsters were recorded, including the structural composition of each site, size, directional orientation, and depth. To gage the potential for thermally-mediated refuge site selection, we measured the thermal properties of refuge sites. We compared the *actual* refuge site (one actually used by a Gila monster) to two additional sites; a *paired* site that was visually similar to the actual refuge with similar width, height, depth, and structural properties, and a *random* site that was sufficient to serve as a refugia but did not necessarily have similar structural properties, dimensions, or directional orientation. This allowed us to assess the potential refugia that are available on the landscape to those actually used by Gila monsters. For each site we measured width, height, maximum depth, and directional orientation (azimuth) of the refuge opening. After Gila monsters left the shelter, we then inserted temperature-recording dataloggers and recorded temperatures every 10 minutes for 72 h.

On-the-ground activities were conducted by a combination of seasonal research technicians, graduate students, and local volunteers assisting as needed. New localities for Gila monsters were gathered from reports to NDOW, social media websites, and by directly contacting individuals who had recently encountered a Gila monster in the field. When we observed a lizard from a new locality, we recorded the location (GPS), measured the individual for size, body weight, and morphometrics, and took a blood sample for genetic analysis. All observations we also added to the NDOW database of species occurrences.

Results and Evidence of Results

A detailed presentation of results is presented in each of five sections contained within this report (attached).

Discussion

The observed home range estimates are similar to the only previous study of Gila monsters in Nevada with reported home ranges averaging 64.2 ha (Gienger 2003). Gila monsters in Nevada appear to have larger home ranges than 34.8 ha reported for individuals in SW Utah (Beck 1990), 36.5 ha for individuals in Arizona (Gallardo 2003) or 58.1 ha for individuals in New Mexico (Beck and Jennings 2003). It is unknown to what degree the duration of study influences these comparisons; our data are from up to five consecutive seasons, whereas the others were gathered across shorter duration investigations.

There does seem to be evidence for the hypothesis that Gila monsters select refuge sites based on thermal suitability. Appropriate refugia (those actually used) seem to have the dual attributes of being warmer in early Spring, when temperatures are low, and cooler in late Summer when above-ground temperatures are potentially lethal. However, we do not yet know to what degree Gila monsters select refugia for reasons other than temperature, such as social interactions with other lizards or because such sites harbor prey items (typically litters of newborn rodents).

Recommendations

An important future direction will be to evaluate the relationship between Gila monster movement, connectivity of populations across Clark County, and genetic diversity. Because many Gila monster populations are small, there may be important effects of individual dispersal on maintaining genetic diversity among populations. If important travel corridors used for dispersal no longer available, then there will likely be significant reductions to gene flow and genetic diversity. Analysis of landscape connectivity and travel corridors would allow the identification of specific areas that should be targeted to maintain sufficient dispersal, and gene flow.

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Part 1: Spatial ecology, home range, and movements by Gila monsters (*Heloderma suspectum*)

Introduction

Gila monsters (*Heloderma suspectum*) are charismatic reptiles that are valued culturally and medically, yet they remain understudied. Data on their abundance are insufficient to estimate population sizes or trends, and as a result, they are protected throughout their range. Nevada has designated them as a state protected species because they are “rarely observed relative to other species”, indicative of the need for more information to design effective conservation measures (Jones 2012). Gila monster protection efforts may also provide an “umbrella” of protection for other species such as chuckwallas (*Sauromalus ater*), which are of special concern in Nevada due to pet trade collection and habitat loss, and the critically endangered Mojave Desert tortoise (*Gopherus agassizii*) which faces widespread habitat degradation and destruction (Nevada Wildlife Action Plan Team 2012). Each of these species are long-lived reptiles with similar habitat preferences. Understanding space use of Clark County Gila monsters is a first step in identifying their habitat requirements and how these vary among separate populations.

The home range of an animal is defined as “the area traversed by the individual in its normal activities such as food-gathering, mating, and caring for young” (Burt 1943). Home range analysis is one of the most commonly used methods for identifying animal space requirements and is often one of the first attributes to be considered for species persistence. Previous studies of Gila monsters have reported minimum convex polygon (MCP) and kernel density estimator (KDE) home ranges (Beck 1990, Beck and Jennings 2003, Gienger 2003, Kwiatkowski et al. 2008, Ariano-Sánchez et al. 2020). Although these estimators are easy to implement and understand, they assume independence of data points. Because locations are taken at frequent intervals, almost all tracking data are temporally autocorrelated, making them unsuitable for analysis using MCP or KDE methods without data thinning (Noonan et al. 2019).

The autocorrelated kernel density estimator (AKDE) home range estimation method accounts for temporal autocorrelation by first fitting each individual with a model based on the autocorrelation structure of the data (Fleming et al. 2015, Fleming and Calabrese 2017, Silva et al. 2021). It also offers improvements over kernel-based methods (some of which can be applied to KDE), such as corrections for over smoothing, small sample sizes (absolute and effective), and unrepresentative sampling in time (Silva et al. 2021). Without these corrections, estimates may be either negatively or positively biased depending on the data, but KDE estimates tend to be smaller compared to AKDE estimates because unmodeled autocorrelation creates a strong negative area bias that can outweigh bias from other sources (Fleming and Calabrese 2017, Noonan et al. 2019). MCPs and KDEs can result in substantially underestimated home range area and inaccurate utilization distributions. These errors in estimation leave managers ill-equipped to plan effective strategies for species management.

In addition to the estimation technique used to calculate a home range area, it is important to consider the temporal span of the data used for the estimate. Reptiles have been shown to alter spatial use with variation in local climatic conditions, which vary over time periods of seasons to multiple years (Duda et al. 1999, Ariano-Sánchez et al. 2020). Some species exhibit considerable heterogeneity in annual estimates of spatial habitat use regardless of local climate and tend towards high site fidelity (Averill-Murray et al. 2020). For long-lived species such as Gila

monsters, heterogeneity in spatial use compounds over time, leading to cumulative estimates of space use that are greater than any individual year. Therefore, total space required for species persistence is not necessarily represented by an annual home range. Annual estimates of space use are likely too narrow in scope to make general conclusions about movement patterns, which are necessary to meet long-term management objectives (Allen and Singh 2016). To facilitate a robust understanding of the spatial ecology of Gila monsters in Clark County, we calculated both annual and cumulative estimates of home range.

Methods

Study sites. Data were collected at two locations in Clark County (referred to as sites A and C). Both sites are within the Mojave Desert and receive less than ten inches of rain annually (Roof and Callagan 2003, Hereford et al. 2006, Western Regional Climate Center 2007). The elevation is generally between 610 and 1,520 m; the field sites lie at 400-900 m and 1,000-1,500 m respectively. Site A is sparsely vegetated, primarily by creosote (*Larrea tridentata*), white bursage (*Ambrosia dumosa*) and brittlebush (*Encelia farinosa*). Site C has a spring which supplies water most of the year, encouraging continual and diverse vegetation growth. Dominant species include creosote, blackbrush (*Coleogyne ramosissima*), white bursage, Anderson thornbush (*Lycium andersonii*) and hedgehog cacti (*Echinocereus engelmannii*).

Data collection. Spatial data were collected using radio telemetry. Data collection occurred primarily between April and August during the Gila monsters activity and breeding seasons (Beck 2005). Individuals were located once to twice per day at site A, and about once per week at site C. Study durations were 4 and 5 years respectively and tracking of individuals varied from 1-5 years. Animals were surgically implanted with a 15 g radio transmitter (Holohil Inc.) that allowed us to follow each individual for up to 16 months before needing replacement. Individuals were kept overnight following their surgery and released the following day at the site of capture. Telonics telemetry antennas and receivers were used to locate the study individuals and locations were recorded using a Garmin GPS.

Data analysis. All analyses were conducted with the R language for statistical computing using the package *amt* for home range estimates. Minimum convex polygon (MCP) and kernel density estimator (KDE) home range estimation methods were used in previous studies, and thus were calculated here for historical comparisons. Autocorrelated kernel density estimators (AKDE) are robust to irregular sampling regimes, small sample sizes (absolute and effective), and temporal autocorrelation (which is present in nearly all animal tracking data; Fleming and Calabrese 2017, Fleming et al. 2019, Noonan et al. 2019, Silva et al. 2021). AKDE estimates were calculated as a measurement of each individual home range area. Home ranges were estimated on both a cumulative and annual scale for individuals with at least 30 observations per year. Individual movement distances were calculated to examine annual and seasonal variability in activity and movement trajectories.

Table 1-1. Cumulative estimates of home range areas (hectares) for two study populations in Clark County. Estimators are mean and standard deviation for Minimum Convex Polygons (MCP), 95% Kernel Density Estimates (KDE), and Autocorrelated Kernel Density Estimates (AKDE).

Population	Estimator	Mean (ha)	SD (area)
A	MCP	100.9	88.6
A	KDE	138.5	138.2
A	AKDE	149.8	111.5
C	MCP	30.7	29.1
C	KDE	64.5	56.0
C	AKDE	58.3	55.1

Table 1-2. Cumulative home range estimates (hectares) for 31 individuals from two study populations in Clark County.

Animal ID	n	AKDE (ha)	KDE (ha)	MCP (ha)
A02	831	131.0	150.5	158.0
A04	777	44.2	45.7	41.0
A06	216	7.0	8.6	6.5
A09	802	109.6	116.4	109.9
A11	535	180.2	169.3	152.0
A13	905	42.4	52.5	45.7
A15	327	166.4	103.5	60.5
A17	510	418.0	525.7	325.8
A19	916	84.6	100.4	75.8
A23	92	159.4	25.7	7.5
A27	347	260.9	239.6	152.8
A35	748	193.9	124.2	75.5
C03	458	27.6	35.2	19.4
C04	187	47.5	53.2	32.1
C06	147	54.1	61.2	34.4
C07	101	24.7	28.6	12.5
C08	185	87.4	74.0	26.4
C09	242	260.0	243.1	127.2
C11	99	14.0	16.7	7.9
C12	107	9.8	13.5	6.4
C13	349	108.5	145.2	82.5
C15	293	21.3	24.3	15.3
C16	91	57.7	71.5	29.4
C18	71	60.9	66.9	26.2
C20	130	38.0	52.2	29.1
C21	45	62.3	130.1	30.5
C22	67	30.7	19.6	8.6
C24	185	60.2	75.2	43.1
C25	232	48.1	50.2	24.3
C29	44	23.0	21.9	5.7
C31	144	71.1	42.3	22.9

"A" and "B" within Animal ID represent two different populations

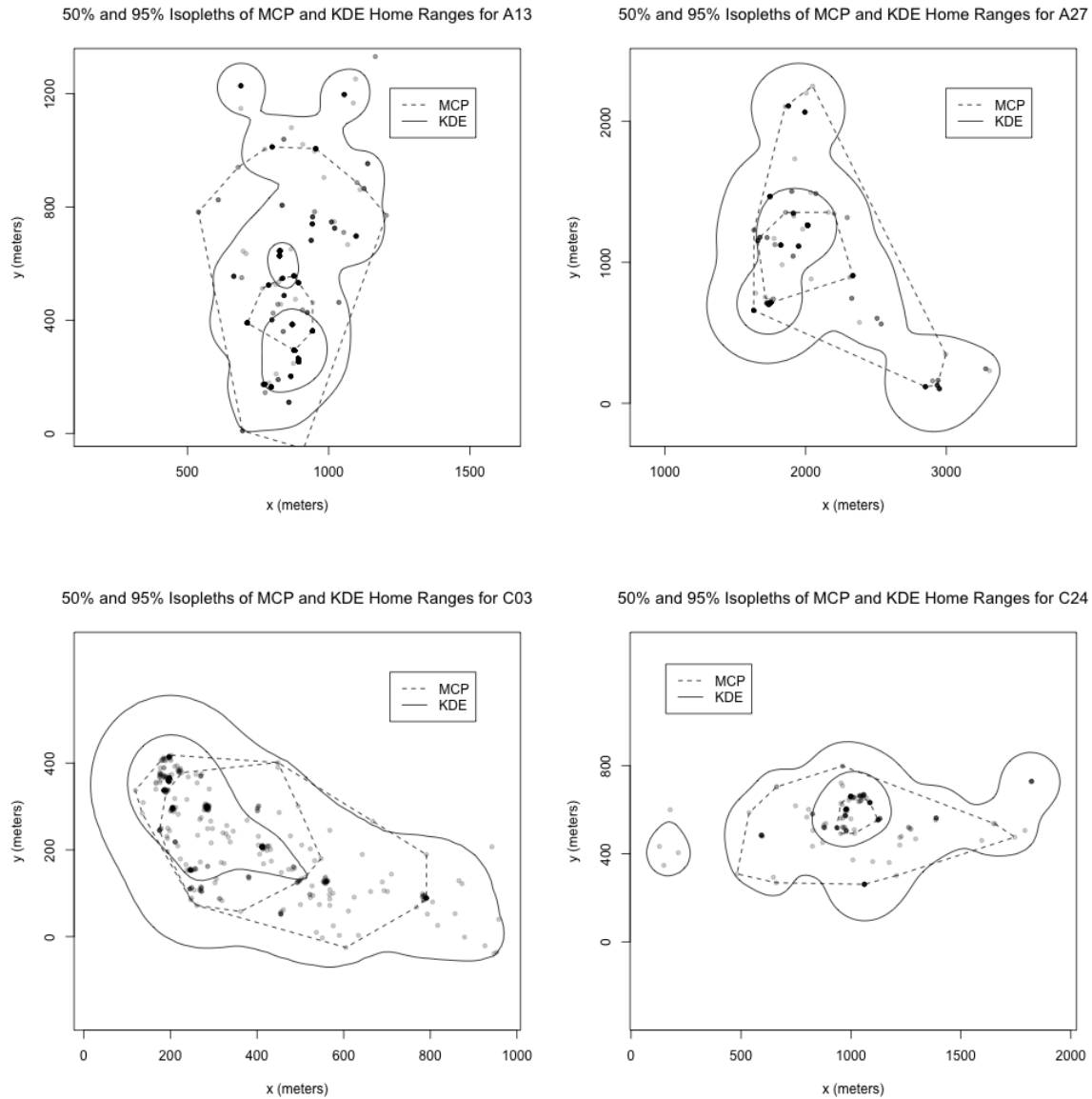


Figure 1-1. Example home range estimates for four Gila monsters monitored in Clark County. Estimates are from two populations (A and C) and show both 50% and 95% Minimum Convex Polygon and 50% and 95% Kernel Density Estimates. Note that the techniques give differing spatial estimates for habitat use.

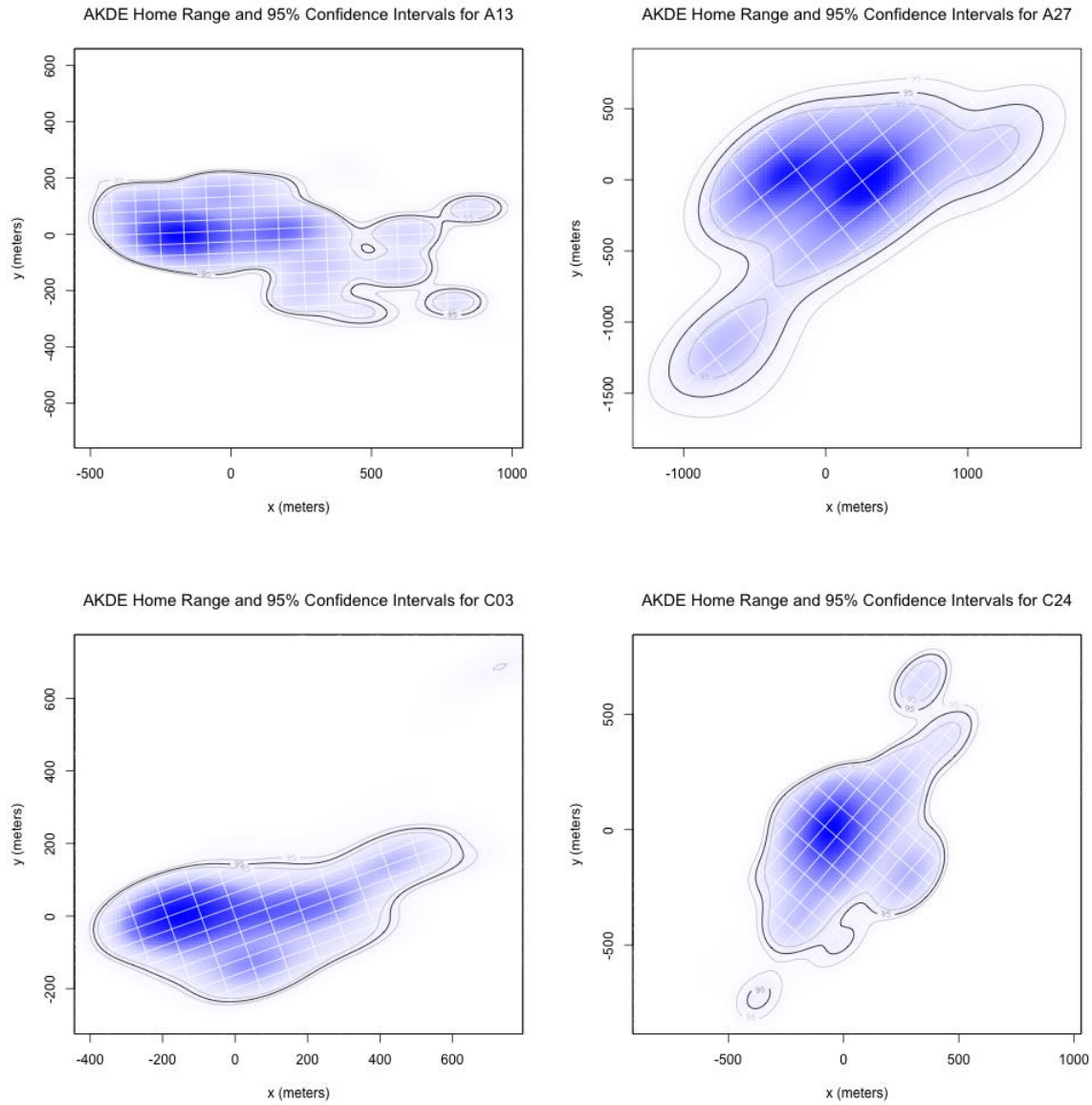


Figure 1-2. Example Autocorrelated Kernel Density Estimates of home range for four Gila monsters monitored in Clark County. Estimates are from two populations (A and C). Darker areas shaded in figures represent parts of the home range with a higher probability of use.

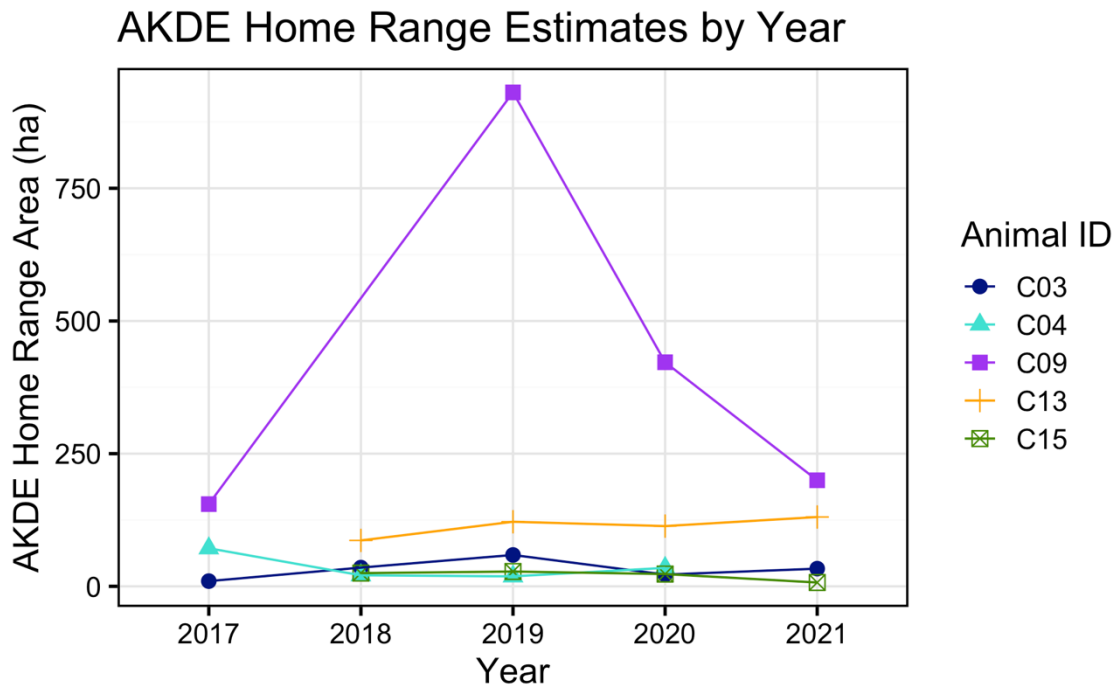
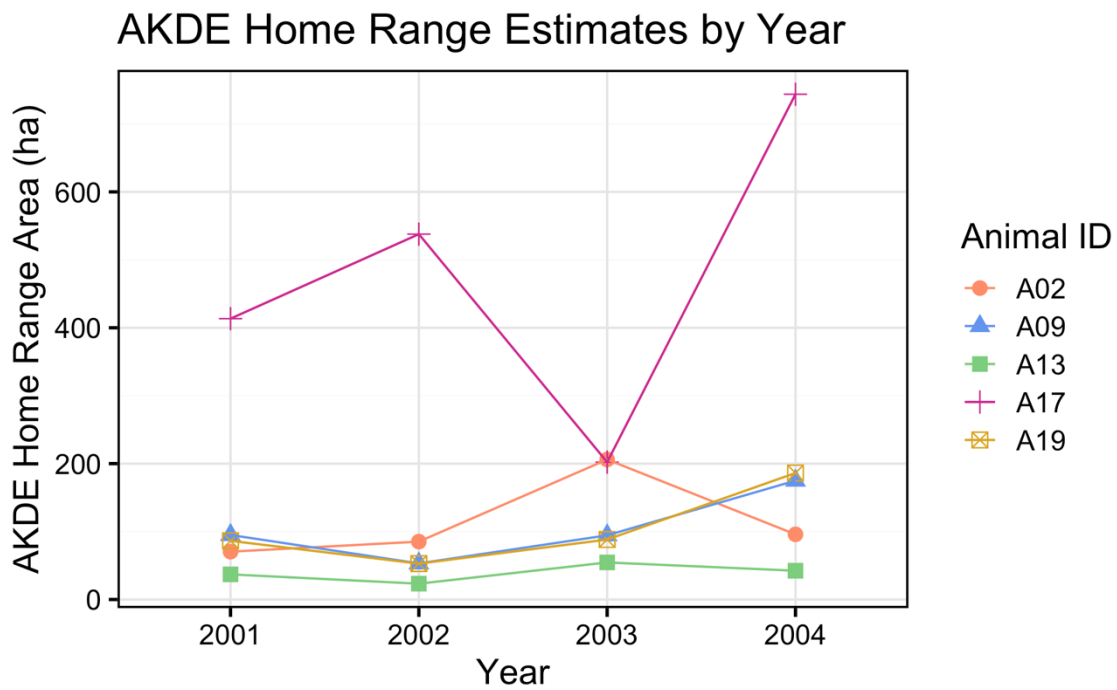


Figure 1-3. Representative Autocorrelated Kernel Density Estimator home range areas for 10 Gila monsters tracked for four years or more in Clark County. Estimates are from two populations (A and C).

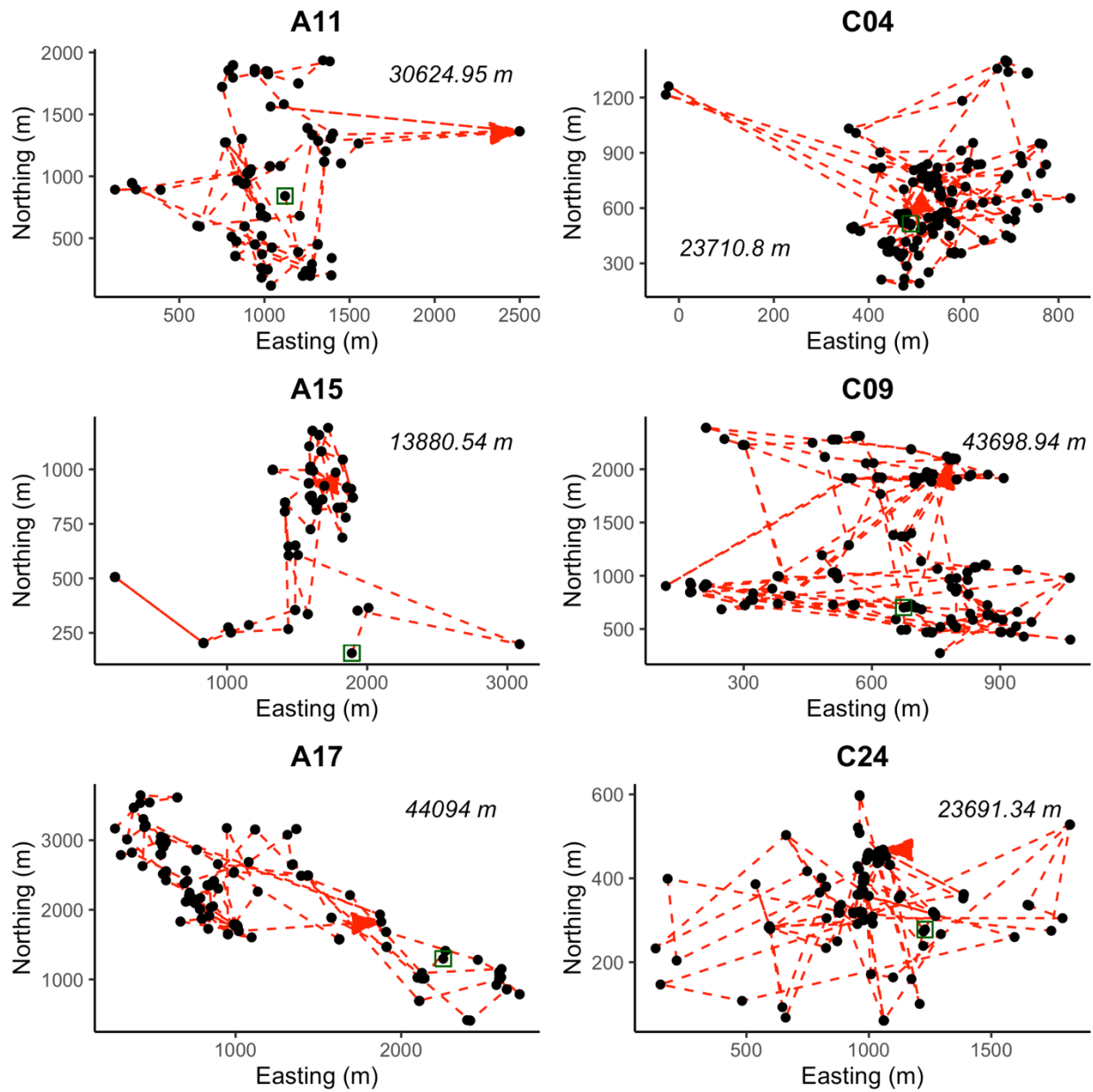


Figure 1-4. Example movement trajectories for six individuals tracked at two study sites in Clark County. Movement estimates are cumulative for up to five years for each individual.

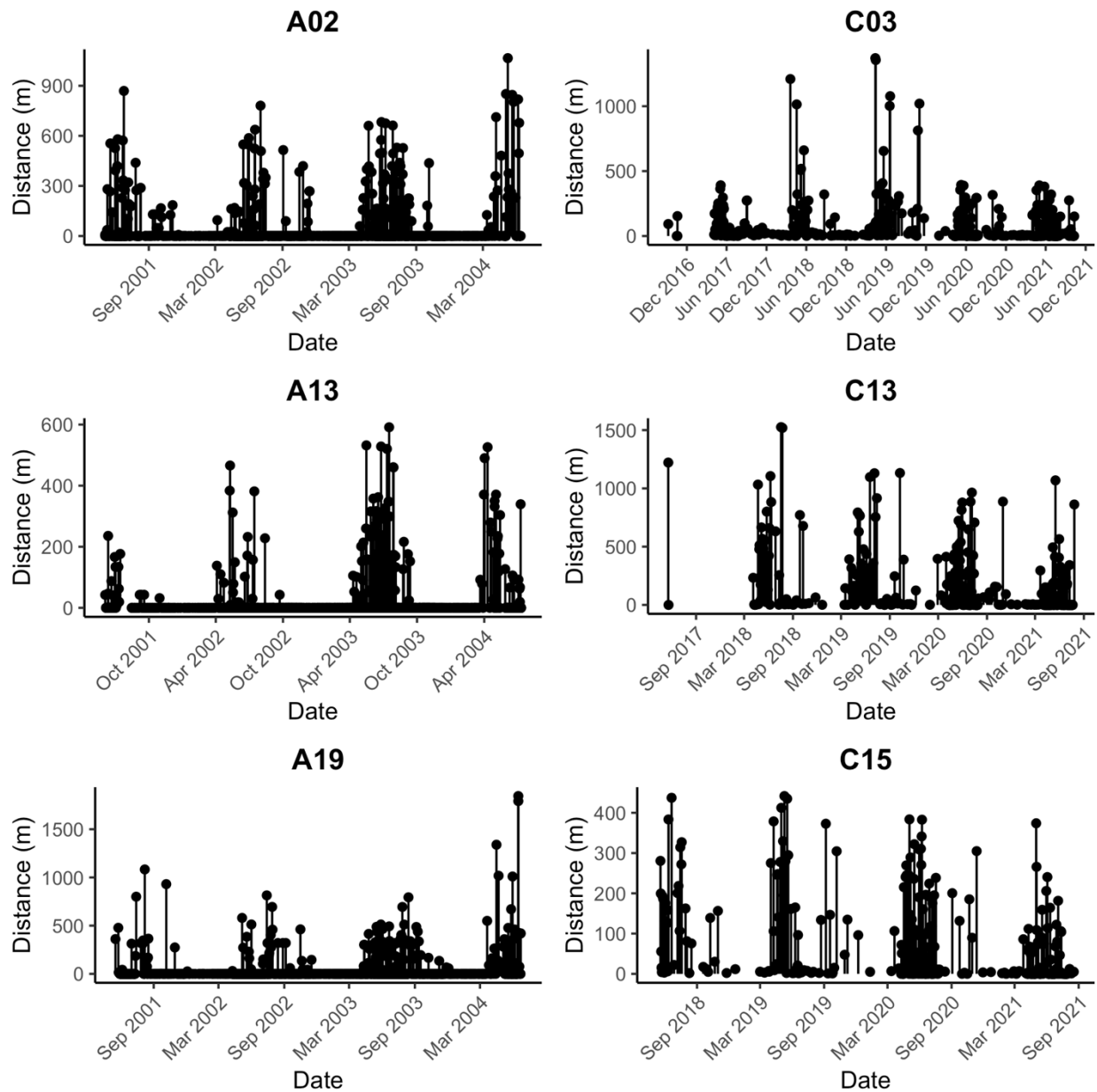


Figure 1-5. Multi-year movement frequencies and distances traveled for six Gila monsters tracked at two locations in Clark County. Data show total movements for up to five years of monitoring.

Table 1-3. Annual estimates of home range for Gila monsters tracked at two study populations (A and C) in Clark County. Estimators are 95% Minimum Convex Polygons (MCP), 95% Kernel Density Estimates (KDE), and Autocorrelated Kernel Density Estimates (AKDE). Only individuals with at least 30 observations per year are included in analyses.

Animal ID	Year	n	AKDE (ha)	KDE (ha)	MCP (ha)
A02	2001	143	70.4	87.3	36.6
A02	2002	283	85.2	91.3	47.4
A02	2003	331	206.1	214.9	159.1
A02	2004	74	95.9	124.0	57.7
A04	2001	140	48.3	56.6	39.4
A04	2002	344	17.1	13.9	11.2
A04	2003	292	67.7	67.9	53.4
A06	2001	124	14.5	17.3	6.5
A09	2001	108	95.0	102.6	47.5
A09	2002	239	53.1	65.4	22.3
A09	2003	377	94.5	92.4	54.7
A09	2004	78	175.0	224.4	115.1
A11	2002	120	8.7	5.5	3.1
A11	2003	324	146.5	172.7	92.2
A11	2004	65	202.1	263.3	159.2
A13	2001	94	37.0	22.8	5.7
A13	2002	301	23.3	32.7	13.5
A13	2003	368	54.6	78.2	61.6
A13	2004	142	42.4	30.9	14.4
A15	2002	99	282.7	156.7	55.8
A15	2003	223	38.0	29.9	19.3
A17	2001	53	413.4	211.1	36.1
A17	2002	123	537.8	718.8	177.4
A17	2003	247	202.2	231.5	117.7
A17	2004	87	743.7	711.2	233.5
A19	2001	127	86.4	72.3	34.3
A19	2002	292	52.8	48.6	31.7
A19	2003	396	88.3	107.9	58.8
A19	2004	101	186.2	226.6	65.4
A23	2001	92	159.5	25.7	7.5
A27	2003	246	276.9	254.8	150.0
A27	2004	101	283.1	224.0	70.9
A35	2002	292	44.2	40.5	21.4
A35	2003	379	133.8	116.7	69.3
A35	2004	77	519.8	442.8	172.2

C03	2017	81	9.8	16.1	6.1
C03	2018	63	35.3	57.2	8.7
C03	2019	63	59.1	101.6	32.8
C03	2020	110	22.1	29.5	12.2
C03	2021	138	33.3	37.1	17.3
C04	2017	57	71.7	98.3	31.8
C04	2018	38	20.8	33.4	13.1
C04	2019	33	18.8	35.5	8.0
C04	2020	56	34.8	35.4	11.6
C06	2017	56	73.3	94.2	35.6
C06	2018	68	40.2	44.3	20.3
C07	2017	52	23.7	27.1	9.8
C07	2018	45	25.5	31.4	10.3
C08	2018	33	30.8	21.9	5.8
C08	2019	31	34.4	43.5	17.4
C08	2020	104	21.0	26.3	15.1
C09	2017	30	154.9	257.6	80.7
C09	2019	43	930.7	330.9	104.7
C09	2020	107	422.2	285.4	103.2
C09	2021	46	199.8	80.2	13.0
C11	2018	75	15.4	18.2	7.8
C12	2018	73	8.7	13.6	5.9
C13	2018	55	86.5	172.0	38.6
C13	2019	67	121.7	181.1	46.7
C13	2020	115	113.5	172.9	72.2
C13	2021	109	130.6	143.3	59.9
C15	2018	37	24.9	27.4	10.6
C15	2019	45	27.9	35.2	12.6
C15	2020	105	23.1	24.4	10.6
C15	2021	106	7.2	10.3	4.5
C16	2018	35	94.0	97.2	22.6
C16	2019	48	49.3	64.6	20.6
C18	2019	34	75.1	80.8	19.7
C20	2020	106	38.9	56.5	23.4
C22	2020	48	48.3	11.9	1.2
C24	2020	109	71.7	103.0	57.6
C24	2021	56	21.4	21.2	9.8
C25	2020	111	54.6	58.3	32.2
C25	2021	115	54.4	33.9	12.9
C29	2021	43	16.3	17.4	4.6
C31	2020	54	139.1	117.6	47.9

A and *B* within Animal ID represent two different populations

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Part 2: Body size variation among populations

Introduction

There are many factors, both environmental and evolutionary that can influence variation in the size of individuals of the same species. Environmentally, potential for growth may not be the same across populations due to either limited environmental resources (food, water) or the energetic costs associated with acquiring those resources (MacArthur and Pianka 1966, Spotila and Standora 1985, Kooijman 1986, Nisbet et al. 2000). A species may face different environmental conditions across its range and natural selection may favor larger bodied animals in some environments and smaller bodied animals in others (Bergmann 1848, Allen 1877, Volynchik 2014). Sex can also influence body size within a population through sexual selection (primarily acting on male size) or fecundity selection (primarily acting on female size; Cox et al. 2003). Here, we analyze body size variation of *H. suspectum* in Clark County to determine whether environmental conditions may play a role in determining variation in population body size.

Optimal foraging theory predicts that animals should maximize their net energetic intake by minimizing the energetic costs of foraging (MacArthur and Pianka 1966). At the same time, energy budget theory attempts to quantify the tradeoffs in total energy allocation and how energetic costs influence the potential for growth and reproduction (Spotila and Standora 1985, Kooijman 1986, Nisbet et al. 2000). Combining these theories, if we assume organisms forage optimally, those in environments with less foraging constraints should allocate less of their total energy expenditure to foraging and are likely to be larger than individuals from populations with higher constraints. In other words, animals with easier access to food should grow larger than those who must work harder to acquire it.

This especially is relevant for Gila Monsters as they are long lived, living 17+ years in the wild (Beck 2005), so the effect of indeterminate growth over their lifetime is potentially more pronounced than in short lived species. *H. suspectum* are specialist nest predators that spend their time foraging widely for the eggs of ground nesting birds and reptiles, and the altricial nestlings of small mammals (Gienger and Tracy 2009). Additionally, thermal constraints of their environment are also especially important because they are surface foragers who retreat to fossorial shelters that act as thermal refugia when surface temperatures are outside their preferred range (Beck 2005). This means *H. suspectum* in more thermally challenging parts of their range are forced to allocate more of their energy to actions like thermoregulating and acquiring food, leaving less energy available for growth.

Variation in environmental conditions is often linked to spatial gradients in latitude and elevation, such as a decline in temperature as you move away from the equator or up in elevation (Gaston 2000, Brown et al. 2004, Brown and Sibly 2006, Pincheira-Donoso et al. 2008). There are several well-known descriptions of this phenomenon and how it relates to intraspecific variation in body size or body proportions, including Bergmann's and Allen's rules, which suggest that animals in cooler climates tend to be larger bodied and have proportionally smaller protruding body parts than those in warmer climates as a means of more efficiently retaining body heat (Bergmann 1848, Allen 1877). However, support for these simplistic rules is often patchy or lacking in ectotherms (Pincheira-Donoso et al. 2008). Other studies suggest that evolutionary influences on body size may be plastic or come secondary to other environmental effects, such as precipitation and primary productivity, which directly influence resource availability at the site level (Lindsey 1966, Rosenzweig 1968, Yom-Tov and Geffen 2006, Volynchik 2014). Understanding how size varies among *H. suspectum* populations is the first step to understanding which environmental parameters are driving variability.

Sexual size dimorphism has long been studied in lizards, with considerable intraspecific variability observed in body size trends (Fitch 1976, 1978, 1981, Schoener et al. 1982, Stamps

1983, Carothers 1984, Stamps et al. 1997, Stamps 1999, Butler et al. 2000, Cox et al. 2003). Two primary hypotheses purport to explain sexual size dimorphism. The ‘Fecundity Advantage Hypothesis’ suggests that larger bodied females have larger maximum clutch sizes, and therefore natural selection would favor larger bodied females (Darwin 1871, Cox et al. 2003). In several instances female body size has not only been correlated with larger clutch size, but has also with more frequent reproductive events (Cox et al. 2003). Comparatively, the ‘Intrasexual Selection Hypothesis’ suggests that mating success in males can be linked to body size. Larger males are more likely to win during bouts of male-male competition and therefore have better access to breeding females and greater opportunities to pass on genes (Darwin 1871, Cox et al. 2003). Male *Heloderma* engage in ritual combat activities to help structure social hierarchies (Gates 1956, Carpenter 1967; Carpenter and Ferguson 1977, Demeter 1986, Beck 1990; Beck and Ramirez-Bautista 1991, Gienger and Beck 2007). Male *H. suspectum* have proportionally larger heads than females, which likely help them in tests of male-male dominance (Gienger and Beck 2007).

Methods

To assess size variation among and within *Heloderma suspectum* populations in southern Nevada, size measurements were compiled from a variety of collaborative research projects and museum records. Two primary measures were used to assess size, snout vent length (a standard measure of body length in lizards) and body mass. For this analysis, all observations within the county were subset to include only those one or both of these measurements. In instances where the same individual had been measured more than once, only the first observation and measurement of that individual was used. This resulted in 61 individuals within the county to be included in analyses. These records were further broken up into those collected at two long term study sites, Site A and Site C, and other incidental observations recorded within the county. For comparison with Clark County data, additional records were acquired from natural history collections, including observations from Pima County, AZ (N = 178), Washington County, UT (N = 106), and Grant County, NM (N = 13).

Three primary analyses were conducted. The first broke records up by field sites within Clark County to assess how size varies across different populations. The second divides all county records by sex to test for sexual dimorphism in body size. Any records not identified as male, female, or subadults were sorted into a fourth ‘unknown’ category but still included in the analysis. Clark County records were compared to those from other states to test for state differences in body size. For each analysis, two tests were performed to analyze how body length and mass differ among categories. A multiple regression analysis was used to test the relationship between mass and body length, and if this differs among the given categorical predictors.

A Shapiro Wilks test was used to test for normality of data prior to performing statistical tests. When data were normally distributed, ANOVA analysis of variance were used to compare means among categories; data not meeting normality assumptions were analyzed using a Kruskal-Wallis test. When main effects were significant, Tukey’s pairwise t-tests were used to compare the means of individual groups. For the multiple regression analysis, normality assumptions for models were visually assessed using the *autoplot* function in R and relationships between mass and body length were assumed to be linear.

Results

There was no difference in mean size of *H. suspectum* across study sites within Clark County using either the individuals body length (SVL; $F_{2,58} = 0.27$, $P = 0.76$) or mass ($F_{2,55} = 0.99$, $P = 0.38$) as a metric of comparison.

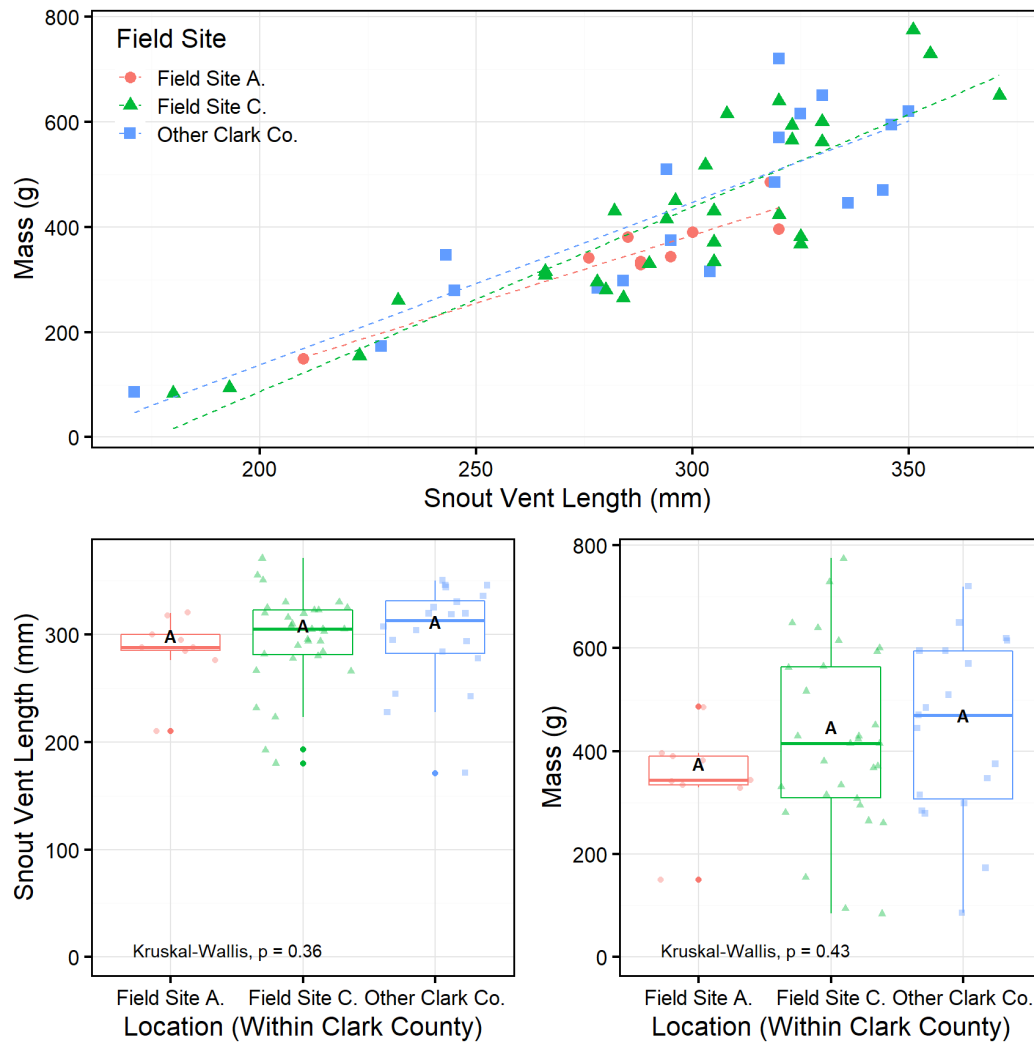


Figure 2-1. Comparison of body size (measured as Snout to Vent length) for Gila monsters in Clark County.

There was a significant effect of sex on body size ($F_{3,57} = 7.3376$, $P < 0.01$) and mass ($F_{3,54} = 7.79$, $P < 0.01$). A Tukey's pairwise post-hoc test revealed that subadults had on average smaller body sizes than all other groups (Subadult-Female: 71.8 mm, $P = 0.002$, Subadult-Male: 80 mm, $P < 0.001$, and Unknown-Subadult: 50.16 mm, $P = 0.039$). On a pairwise basis, males were found to be significantly heavier than subadults and those of unknown sex (307.6 g and 168 g respectively, $P < 0.01$).

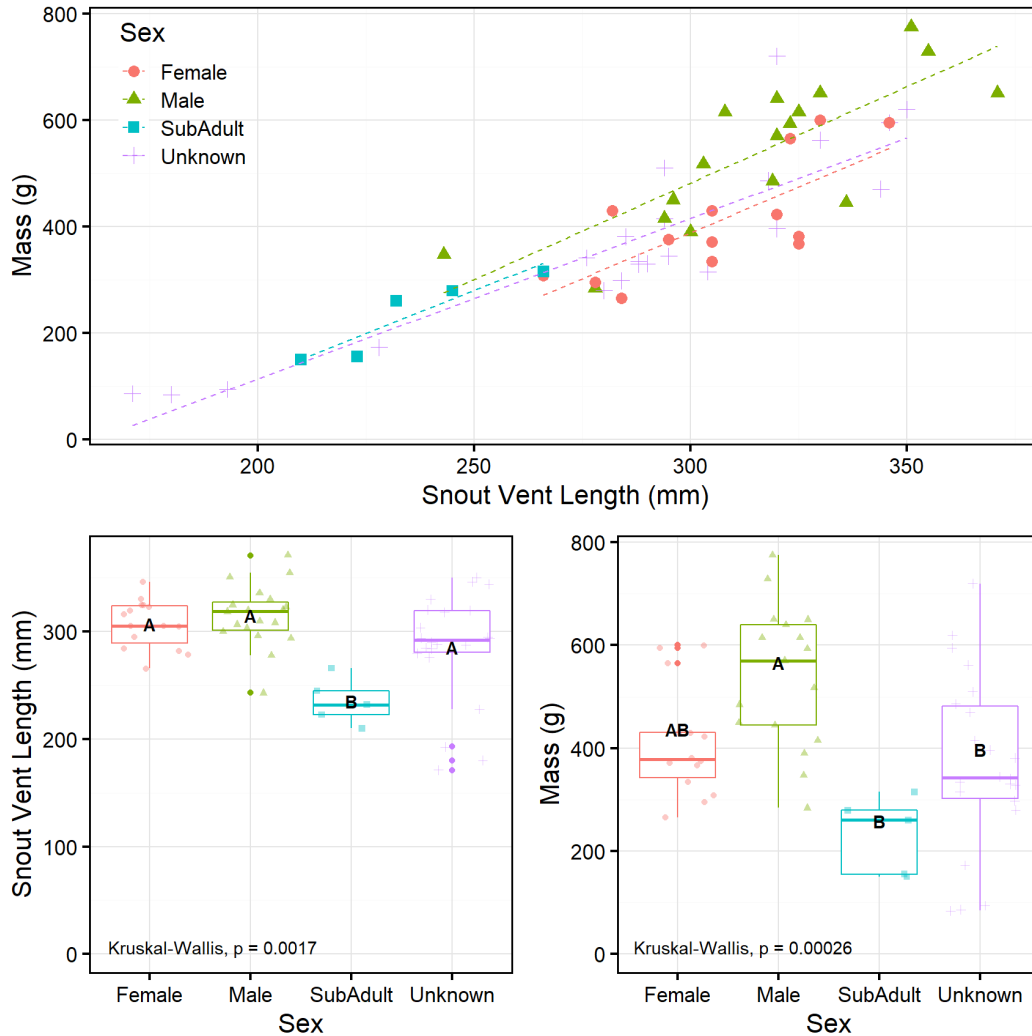


Figure 2-2. Comparison of Gila monster body size among age and sex groups.

A significant difference was found between the body size of *H. suspectum* from Clark County and other populations across their range ($F_{3,277} = 24.13$, $P < 0.001$). On a pairwise basis, *H. suspectum* from Clark County had larger body sizes than those from Pima County, Arizona (50.07mm, $P < 0.001$) but otherwise were no difference from Washington County, Utah or Grant County, New Mexico. No significant difference in mass was found between state populations ($F_{3,137} = 1.44$, $P = 0.23$).

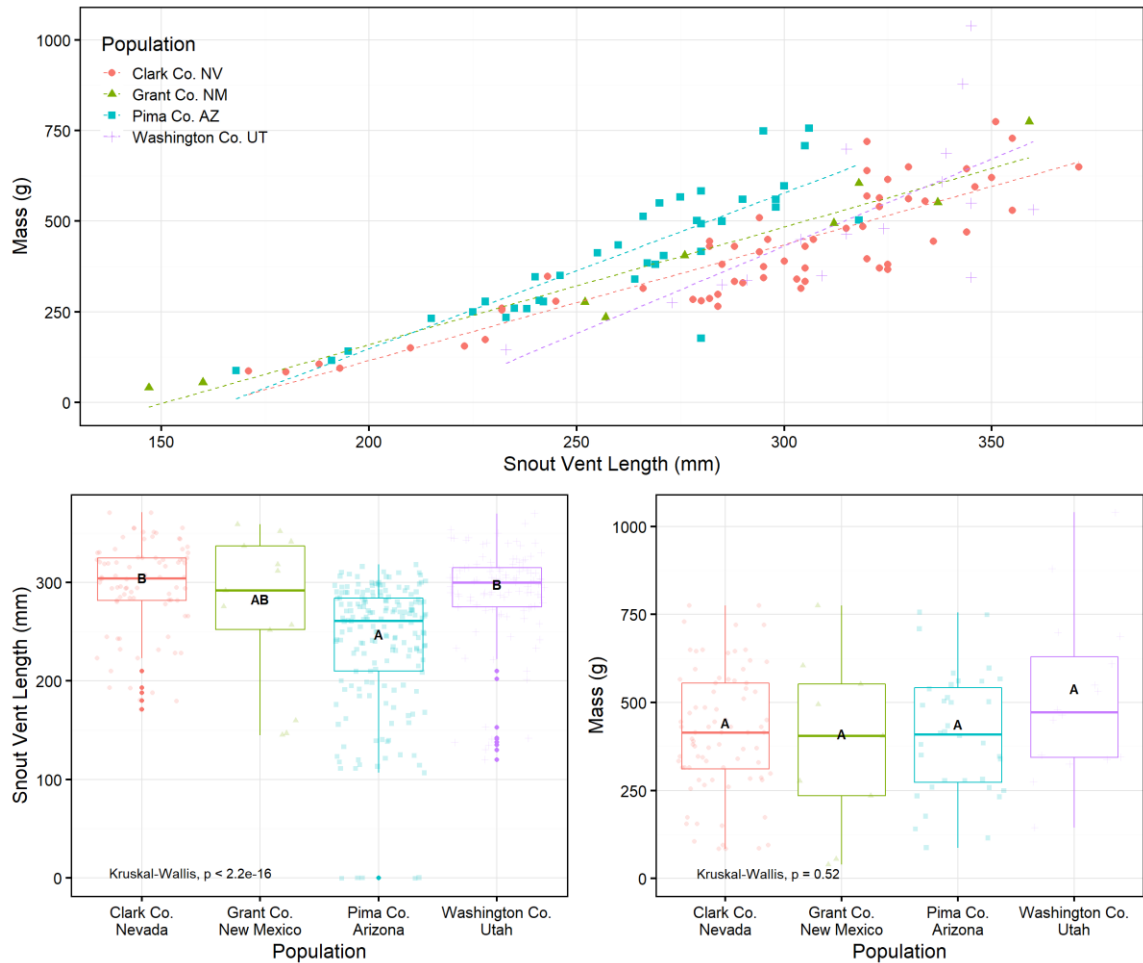


Figure 2-3. Comparison of Gila monster body size and body mass for Clark County Gila monsters and those from other populations in New Mexico, Arizona, and Utah.

There was a significant relationship between body size and mass, after accounting for site within Clark county ($F_{1,52} = 159.6$, $P < 0.001$), sex ($F_{1,50} = 195.53$, $P < 0.001$), and populations outside of Nevada ($F_{1,133} = 473.39$, $P < .001$). For Clark County monsters, an increase in one mm in body length predicts an average increase in 0.25 grams in mass (slope = 0.243, intercept: 192.43, $t = 30.68$, $P < 0.001$). No interactive effects were found between mass and site ($F_{2,52} = 0.89$, $P = 0.42$), or between mass and sex ($F_{3,50} = 1.83$, $P = 0.154$). A possible interactive effect was found between mass and state ($F_{3,133} = 11.892$, $P < 0.001$). As body size increases, mass of animals in Pima County, AZ and Washington County, UT increases at a faster rate than those in Clark County (Slope: -0.07 and Slope: -0.14 respectively, $P < 0.01$ for both).

Table 2-1. Count of individuals used in comparisons of body size across Clark County.

	Field Site A. (N=9)	Field Site C. (N=32)	Other Clark Co. (N=20)	Total (N=61)
Female	0 (0.0%)	13 (40.6%)	2 (10.0%)	15 (24.6%)
Male	1 (11.1%)	10 (31.2%)	8 (40.0%)	19 (31.1%)
SubAdult	1 (11.1%)	3 (9.4%)	1 (5.0%)	5 (8.2%)
Unknown	7 (77.8%)	6 (18.8%)	9 (45.0%)	22 (36.1%)

Table 2-2. Collection and measurement information for individuals used in comparisons of body size across Clark County.

Lizard_ID	Sex	Collection_Date	SVL	Mass_grams	Tail_Volume	Site
Other HESU 1	Male	1952-06-27	307	NA	NA	Other Clark Co.
Other HESU 2	Unknown	1994-05-22	320	720	NA	Other Clark Co.
A02	Unknown	2001-05-05	276	341	NA	Field Site A.
A03	SubAdult	2001-05-11	210	150	NA	Field Site A.
A17	Male	2001-05-28	300	390	NA	Field Site A.
A09	Unknown	2002-04-09	320	396	NA	Field Site A.
A13	Unknown	2002-04-18	318	486	NA	Field Site A.
A19	Unknown	2002-05-07	288	329	NA	Field Site A.
A35	Unknown	2003-05-07	295	344	NA	Field Site A.
A15	Unknown	2003-05-19	288	334	NA	Field Site A.
A04	Unknown	2003-11-05	285	381	NA	Field Site A.
Other HESU 3	Unknown	2008-05-22	304	315	NA	Other Clark Co.
Other HESU 4	SubAdult	2009-05-30	245	279	NA	Other Clark Co.
Other HESU 5	Male	2009-06-01	243	347	NA	Other Clark Co.
B1	Male	2013-04-12	330	650	NA	Other Clark Co.
B2	Unknown	2013-04-22	171	86	358	Other Clark Co.
B4	Unknown	2013-04-29	350	620	67	Other Clark Co.
B3	Male	2013-04-30	319	485	64	Other Clark Co.
B5	Male	2013-05-01	320	570	NA	Other Clark Co.
Other HESU 6	Male	2013-05-12	278	284	38	Other Clark Co.
B7	Female	2013-06-11	295	375	26	Other Clark Co.
Other HESU 7	Unknown	2013-07-06	284	298	35	Other Clark Co.
B9	Unknown	2013-08-23	346	595	NA	Other Clark Co.
B11	Female	2014-05-13	346	595	NA	Other Clark Co.
B8	Male	2014-09-16	325	615	74	Other Clark Co.
C3	Female	2016-05-13	320	423	51	Field Site C.
C4	Female	2016-05-22	278	295	45	Field Site C.
C5	Male	2016-05-23	351	775	110	Field Site C.
C6	Female	2016-08-02	316	NA	56	Field Site C.
C7	Female	2017-04-05	266	308	45	Field Site C.
Other HESU 8	Unknown	2017-04-17	344	470	70	Other Clark Co.
C8	Male	2017-05-10	303	517	76	Field Site C.
C9	Male	2017-05-25	310	NA	64	Field Site C.
C10	Male	2017-06-01	296	450	66	Field Site C.
C11	Female	2017-08-29	305	371	47	Field Site C.
C12	Female	2017-09-01	305	334	51	Field Site C.
C13	Male	2018-04-04	308	615	72	Field Site C.
C14	Male	2018-05-04	320	640	75	Field Site C.
C15	Female	2018-05-12	330	600	81	Field Site C.
C16	Male	2018-05-16	355	729	102	Field Site C.
C17	Female	2018-05-21	305	430	65	Field Site C.
C18	Female	2018-05-22	282	430	63	Field Site C.
C35	Male	2018-05-24	371	650	91	Field Site C.
C-Stub	Unknown	2018-06-06	330	562	NA	Field Site C.
Other HESU 9	Unknown	2018-07-09	228	173	16	Other Clark Co.
C19	Female	2019-03-26	325	367	38	Field Site C.
Other HESU 10	Male	2019-04-23	336	445	42	Other Clark Co.
Other HESU 11	Unknown	2019-05-08	294	510	75	Other Clark Co.
C20	Unknown	2019-05-18	294	415	55	Field Site C.
C21	Male	2019-05-20	294	415	55	Field Site C.
C22	Female	2019-05-21	323	565	66	Field Site C.
C23	Unknown	2019-06-01	280	280	33	Field Site C.
C24	Male	2019-06-19	323	593	82	Field Site C.
Cjuv1	Unknown	2019-06-21	180	84	10	Field Site C.
Cjuv2	Unknown	2019-07-02	193	94	7	Field Site C.
C25	Female	2019-09-29	325	381	43	Field Site C.
C27	Unknown	2020-04-16	290	330	49	Field Site C.
C30	SubAdult	2020-05-10	232	260	38	Field Site C.
C31	SubAdult	2020-05-10	266	315	40	Field Site C.
C32	SubAdult	2020-05-17	223	155	21	Field Site C.
C29	Female	2021-06-15	284	265	27	Field Site C.

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Part 3: Seasonal differences in shelter selection

Methods

Lizards were tracked and located several times per day throughout the spring and summer (April through September) and 2-5 times per week throughout the fall and winter (October to March). Location was recorded using a handheld GPS (GPS III, Garmin Intl.), and activity type (resting inside a shelter, basking near shelter opening, or surface activity) as well as body temperature was recorded for each observation.

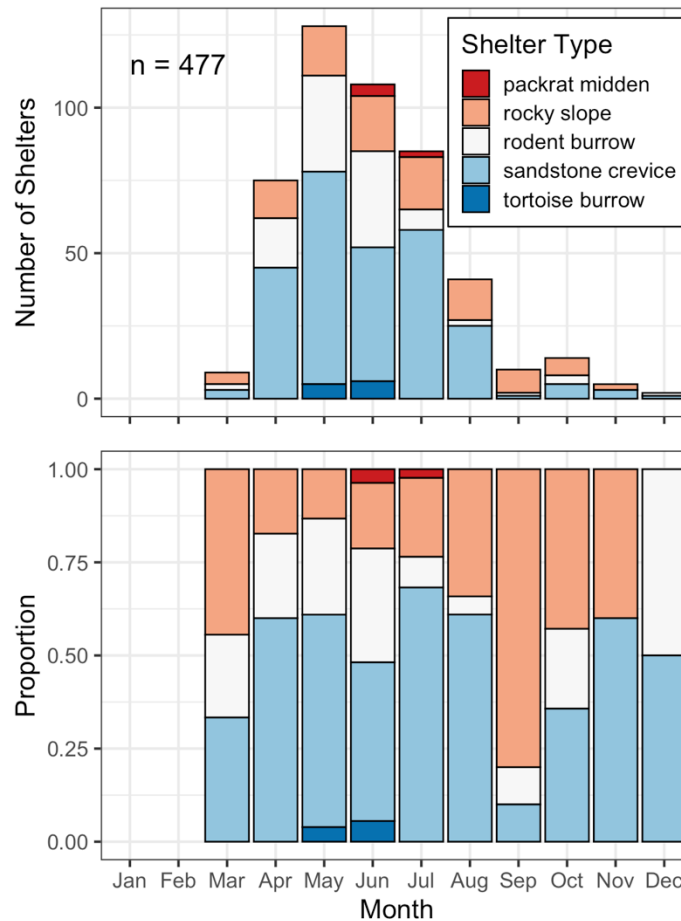


Figure 3-1. Shelter types used by Gila monsters.

Gila monsters do not dig their own shelters. Instead, they use either shelters created by other animals (sometimes modifying the site via excavation) or rocky refuges created by geologic weathering. Shelters used by the lizards were classified as either a rock crevice, rocky slope (debris flow), rodent burrow, or tortoise (*Gopherus agassizi*) burrow. To give an estimate of the structure (rockiness) of each shelter, the roof and floor were each scored (in 0.5 increments) from 1.0 for sandy loam to 3.0 for gravel to 5.0 for solid rock. Directional azimuth and dimensions of the shelter opening were recorded as was the depth of any Gila monster visually observed within a shelter.

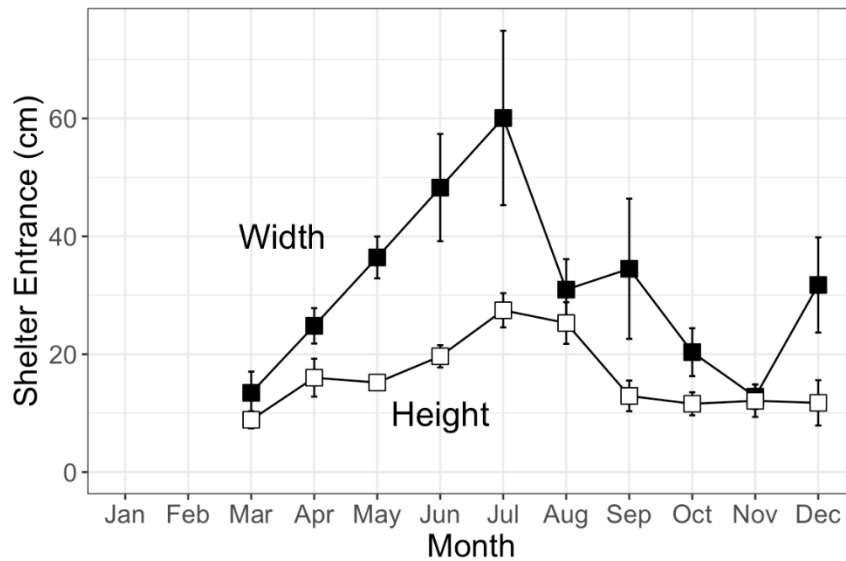


Figure 3-2. Width and height of shelter openings (mean \pm standard error) used by Gila monsters. Lizards use deeper and wider shelters (typically deep rocky caves) during hot summer months (June-July).

Results

Physical structure of shelters (degree of rockiness) varied somewhat by season. Although the rockiness of shelter roofs was not significantly different among seasons (Kruskal-Wallis $H_c = 0.205$, $P = 0.942$), shelter floors varied significantly (Kruskal-Wallis $H_c = 6.713$, $P = 0.043$) and had mean floor scores of 2.1, 1.8, and 2.3 for fall-winter, spring, and summer respectively (i.e. gravelly-loam in all seasons). Shelters with roof or floor scores below 2.0 are typically rodent burrows and are used primarily by Gila monsters during spring foraging. Overall, shelters were associated primarily with sandstone crevices and rocky slopes-rock flows, comprising 61% and 24% of observations respectively. Some shelters were reused by Gila monsters up to 15 times across four years of field study, but most sites were only used 1-3 times.

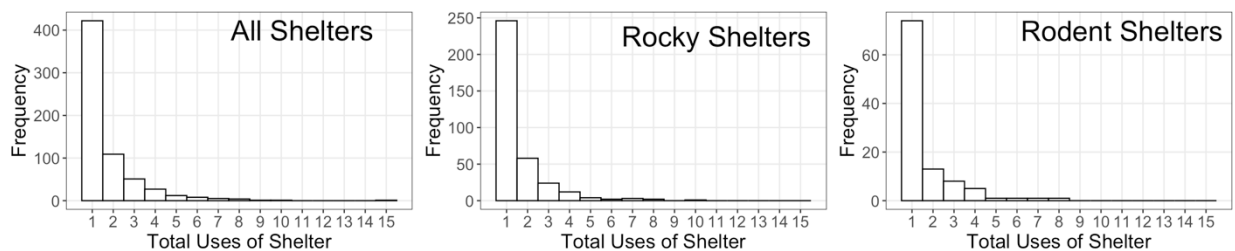


Figure 3-3. Reuse of shelter sites by Gila monsters. Shelters were reused up to 15 times (by several different individuals), but the majority of sites were only reused 1-3 times.

Average depth of shelters (individual means) differed significantly with season (Figure 3-4; $F = 7.820$, $P = 0.005$) and as the thermal environment gets progressively hotter, Gila monsters select successively deeper shelters.

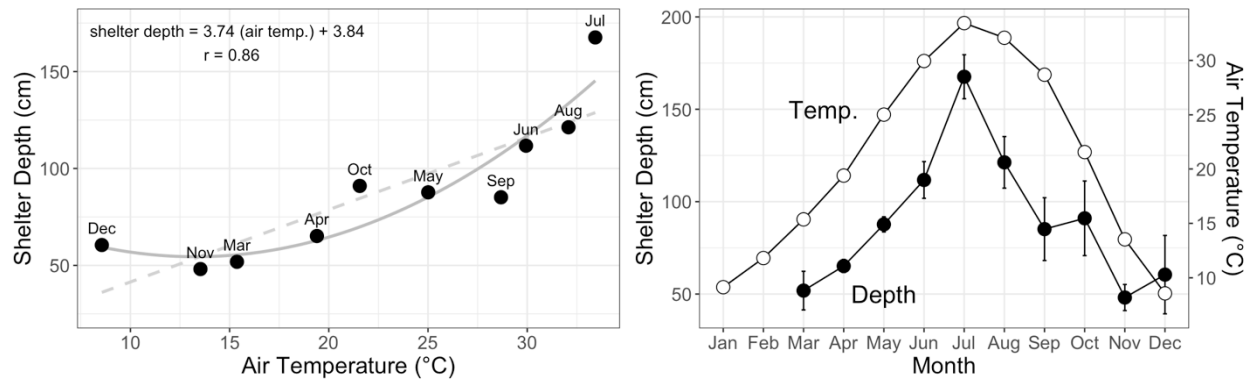


Figure 3-4. Shelter selection in Gila monsters is influenced by temperature. As seasonal temperature become hotter in late Spring and Summer (May, June, and July), Gila monsters chose shelters deeper underground.

Multiple comparisons of means (Tukey-Kramer) show that summer shelters (May through August) were significantly deeper than either fall-winter shelters (those used September through December, $P < 0.05$) or spring shelters (March and April, $P < 0.05$), but fall-winter shelters and spring shelters did not differ significantly from each other ($P > 0.05$). The orientation of the openings (azimuth) of shelter sites did not differ by season, and all seasons had a uniform distribution (Rayleigh's $P > 0.05$; Figure 3-5.).

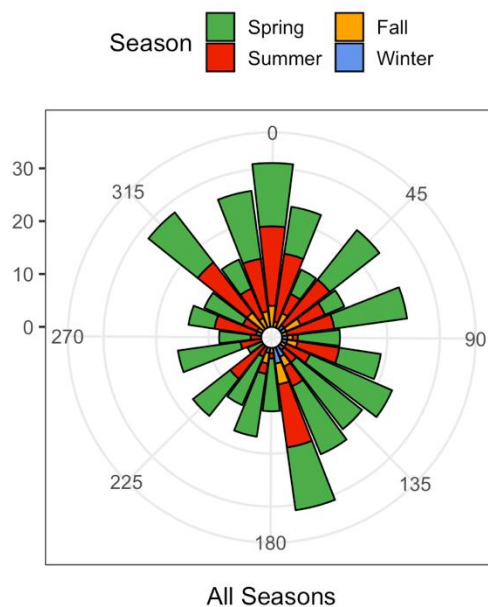


Figure 3-5. Direction of shelter openings chosen by Gila monsters.

Discussion

Microhabitat (refuge site) selection differs seasonally and seems to be influenced primarily by seasonal differences in thermal environments. Gila monsters choose successively deeper shelter sites, over the course of the spring and summer as temperatures get progressively hotter, and shallower sites during early spring and fall when thermal environments are cooler. Shallow refuge sites (<1 m) vary greatly in temperature (Muth 1980, Porter and Tracy 1983), and temperatures in these sites may often surpass the thermal limits of the species. Thus, Gila monsters may be forced to seek deeper shelters (>1 m) as temperatures in shallow sites becomes unsuitable.

The substratum of shelters used by Gila monsters varies with season, and this may be related to Gila monsters using sandy rodent burrows for temporary shelter while they forage in the spring. Rodent burrows were almost only used during the season of greatest Gila monster activity (April to August) when nests of rodents, reptiles, and ground nesting birds are available as prey. Because rodent burrows can be quite shallow, they may offer less thermal refuge. Gila monsters use refuge sites that are constructed by other animals much less extensively (12% rodent burrows and 3% tortoise burrows) than those formed by geologic weathering (85% rocky debris flows or crevices). These “animal made” shelters are more frequently found in loose friable soil and tend to be more ephemeral, so they may not be able to be used year-after-year.

At this study site, roof structure and orientation (rockiness and directional azimuth) of shelters seem to be factors of less importance than that of depth. Seasonal shifts in the micro-climate (temperature and humidity), orientation, slope, and rockiness of shelters have been reported for Gila monsters in western New Mexico (Beck and Jennings 2003) but in southern Nevada Gila monsters may simply respond to surface temperature by selecting deeper refuges to avoid overheating and desiccation.

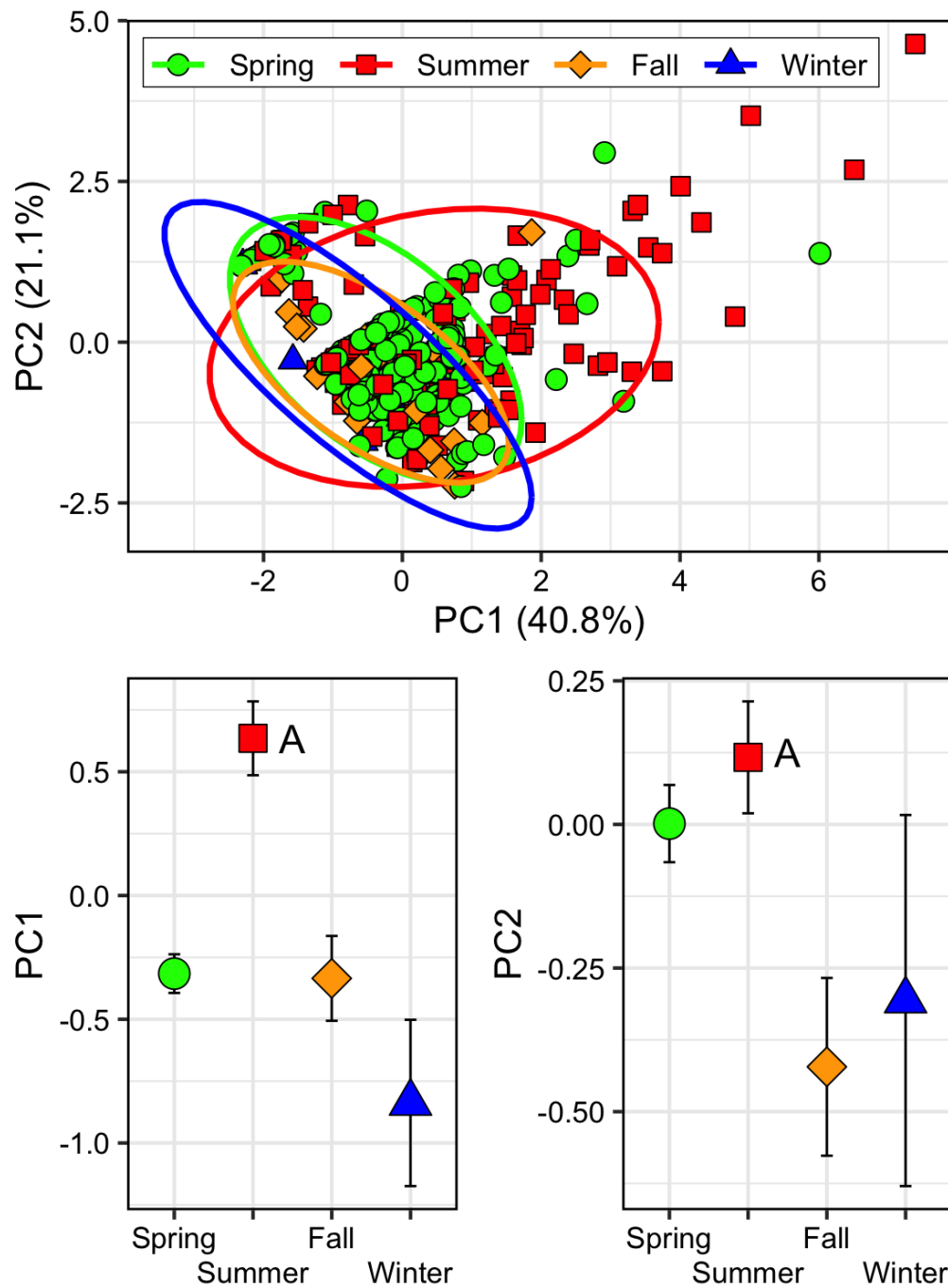


Figure 3-6. Results of multivariate comparison of shelter attributes (Principal Components Analysis). PC axis1 describes a gradient of shelter depth; Gila monsters chose much deeper shelters during the summer when above-ground temperatures were at the annual maximum. PC axis describes a gradient of shelter width and height; there were not strong differences among seasons in shelter width and height.

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Part 4: Thermally mediated refuge site selection

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.

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. 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 avoiding predation (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). While avoiding predation 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 of predation (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; Stellateli 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 4-1). 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 4-1). We found that mean temperatures did not differ among shelter types by month ($F_{2,88} = 2.27$, $p = 0.109$; Figure 4-2); 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 4-2). 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 4-3) 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 4-3), where actual shelters had 5.8 ± 4.7 hours per day within T_{set} , while potential shelters had 3.3 ± 3.9 hours per day within T_{set} ($n = 17$). Random shelters, which had 6.5 ± 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 4-4); 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 4-5). 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°C , compared to 1.76°C for potential shelters, and 2.21°C for random shelters ($F_{2,94} = 10.83$; $p < 0.001$; Figure 4-6). 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 4-7). Standard deviation of the overall mean temperature among shelter types differed by month ($F_{2,88} = 17.24$, $p < 0.001$; Figure 4-6); 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°C and the random shelter to be 1.91°C ($p = 0.014$). In July, mean standard deviations of the overall mean temperature were 0.43°C for actual shelters, 1.49°C for potential shelters ($p < 0.001$) and 1.93°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 , and 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 4-8). 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 4-9).

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 4-10a). 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 4-10b), or \bar{d}_e of a shelter ($t_{45} = 0.110$, $p = 0.913$; Figure 4-10c) 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 gauge 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 4-1. 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 ^A	10.8 ± 4.4 ^A	15.7 ± 8.9 ^B	0.014
Width (cm)	26.8 ± 19.0 ^A	26.9 ± 17.4 ^A	39.6 ± 29.4 ^B	0.003
Depth (cm)	80.5 ± 33.9 ^A	75.8 ± 29.7 ^A	56.1 ± 27.1 ^B	0.000
Roof	4.9 ± 0.6 ^A	4.9 ± 0.6 ^A	4.9 ± 0.5 ^A	1.000
Floor	2.0 ± 1.0 ^A	2.2 ± 1.0 ^A	3.1 ± 1.2 ^B	0.000
Azimuth (°)	173.5 ± 0.7 ^A	174.6 ± 0.8 ^A	191.0 ± 1.3 ^A	0.250
Logger Depth (cm)	72.7 ± 29.4 ^A	69.4 ± 28.3 ^A	48.5 ± 22.5 ^B	0.000

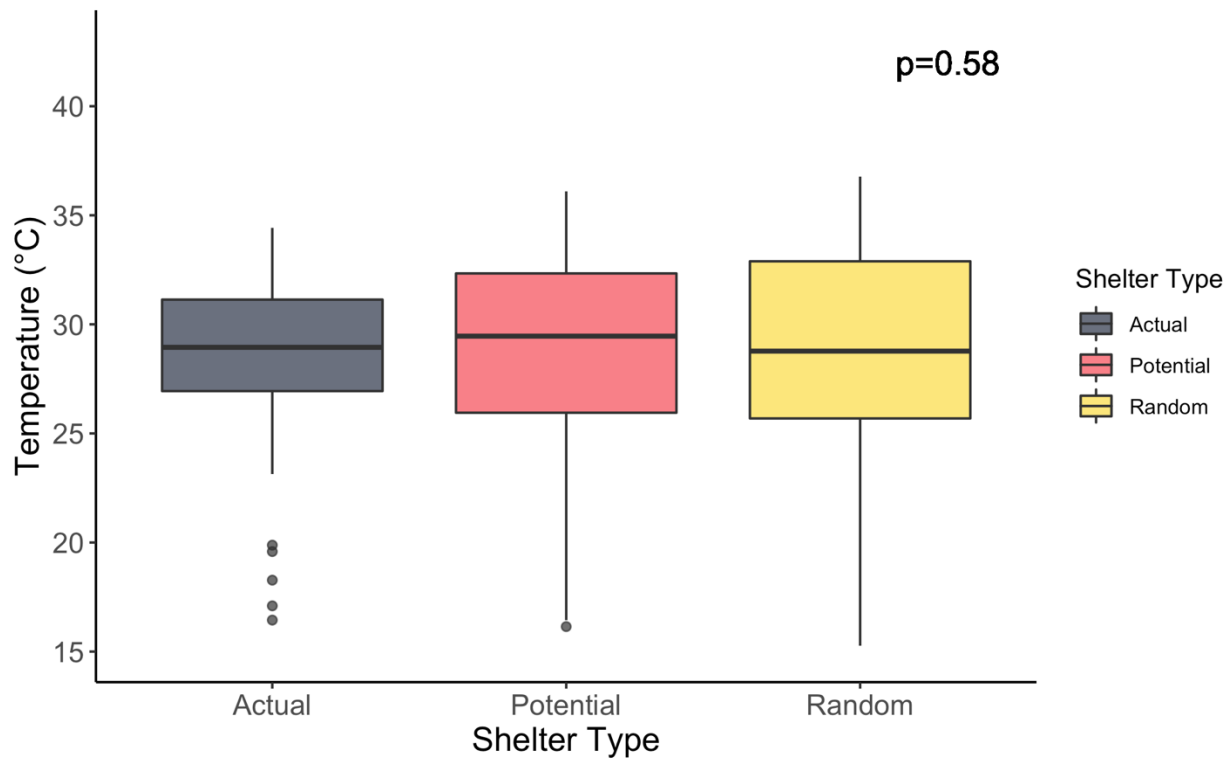


Figure 4-1. Mean temperature by shelter type (n=48 for each) from April-July 2020. Mean overall temperature did not differ among shelter types. Letters over the box plots indicate post-hoc comparisons using a Tukey's Test. Shelter types with the same letter are not significantly different from one another.

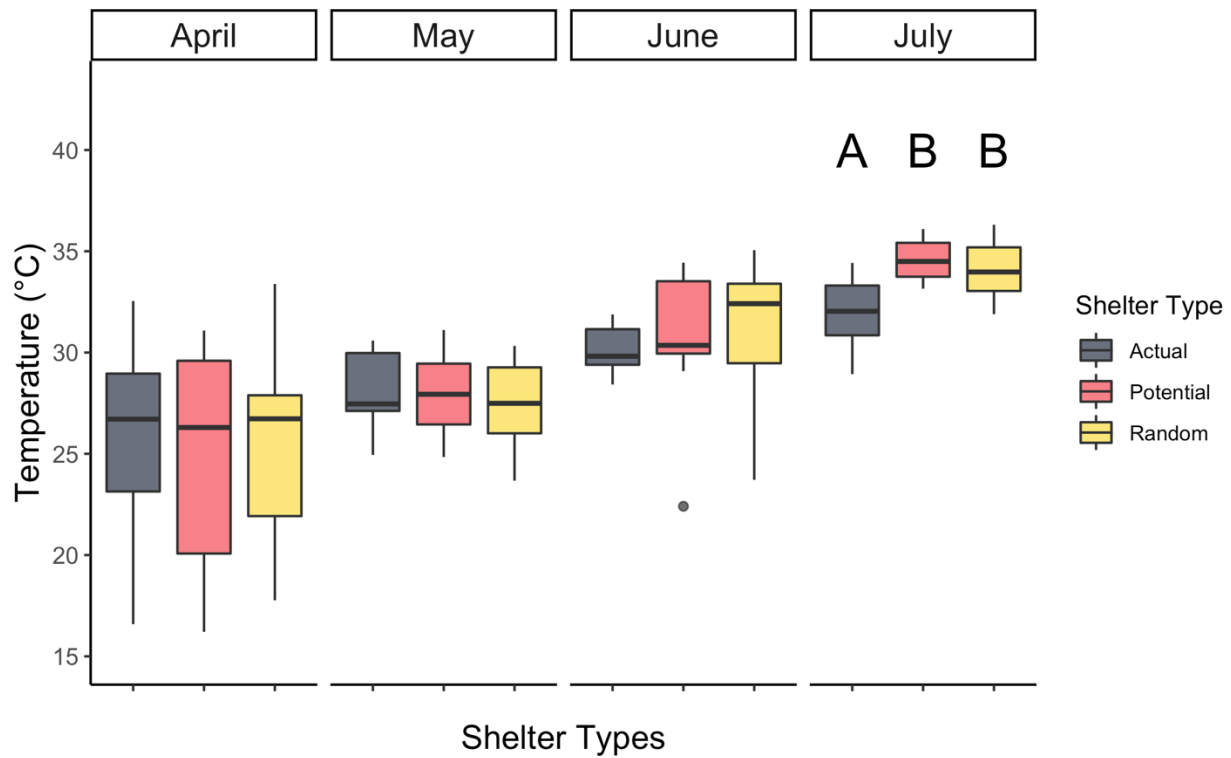


Figure 4-2. Mean temperature (with standard deviation error bars) for each shelter type by month. (n=17 for April, n=13 for May, n=9 for June, n=9 for July). Letters over the box plots in July indicate within-month post-hoc differences using a Tukey's Test. Shelter types with the same letter are not significantly different from one another; shelter types were not significantly different in April, May, June.

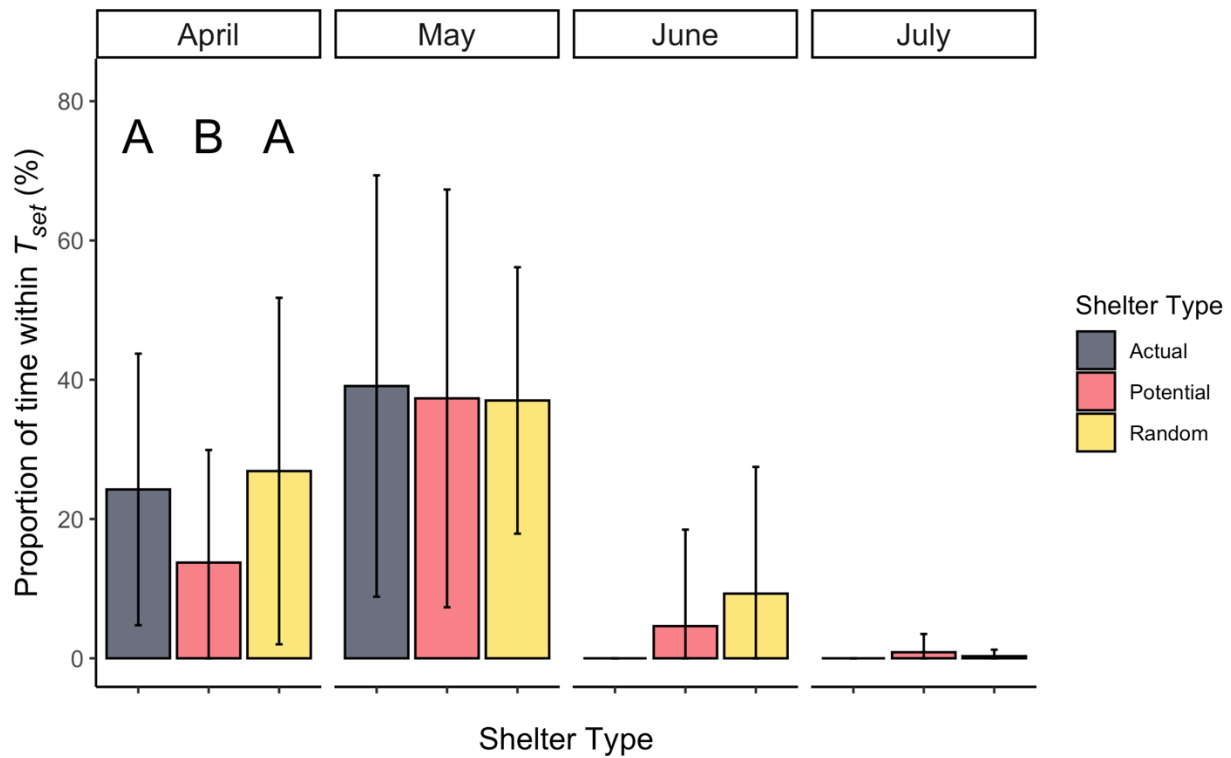


Figure 4-3. Proportion of time (with standard deviation error bars) within the set-point range (T_{set}) by shelter type and by month ($n=17$ for April, $n=13$ for May, $n=9$ for June, $n=9$ for July). Letters over the box plots in April indicate within-month post-hoc differences using a Tukey's Test. Shelter types with the same letter are not significantly different from one another; shelter types were not significantly different in May, June and July.

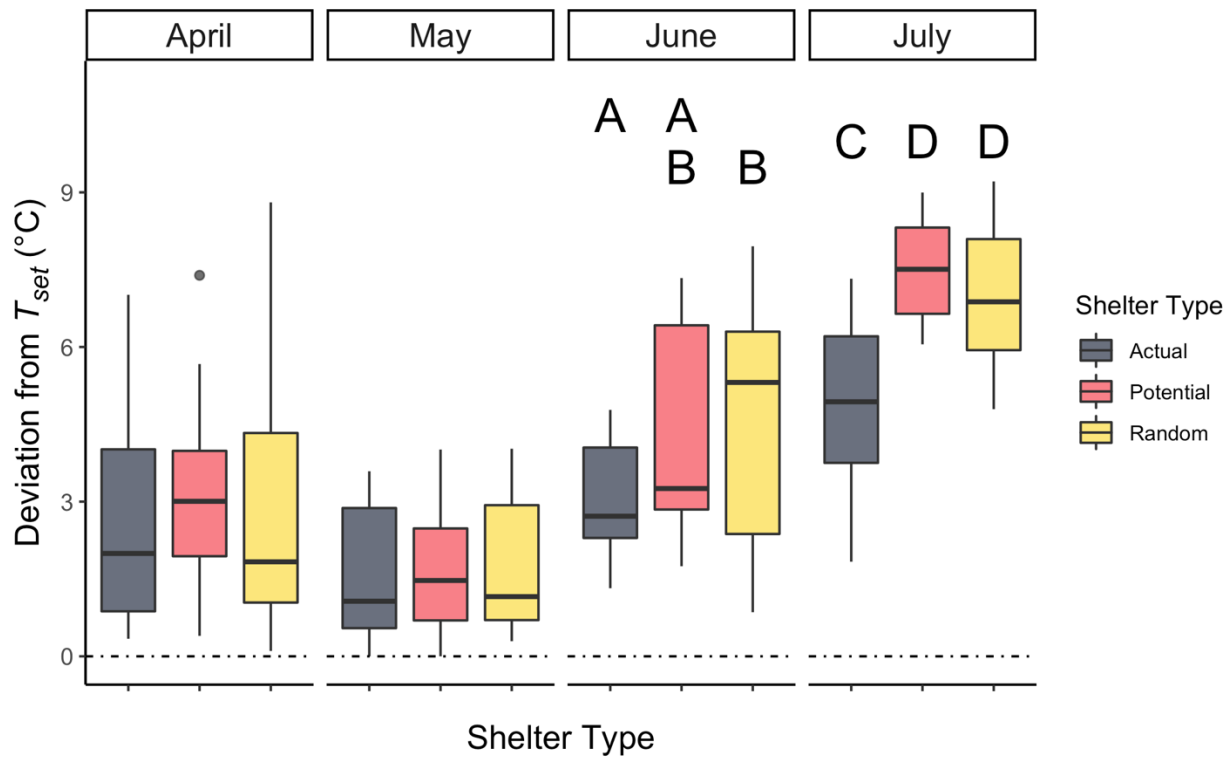


Figure 4-4. Thermal quality of shelters as measured by mean d_e (deviation from thermoregulatory set-point range) across months ($n=17$ for April; $n=13$ for May; $n=9$ for June; $n=9$ for July) with standard deviation error bars. A deviation of 0°C would indicate that the temperature was within the 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.

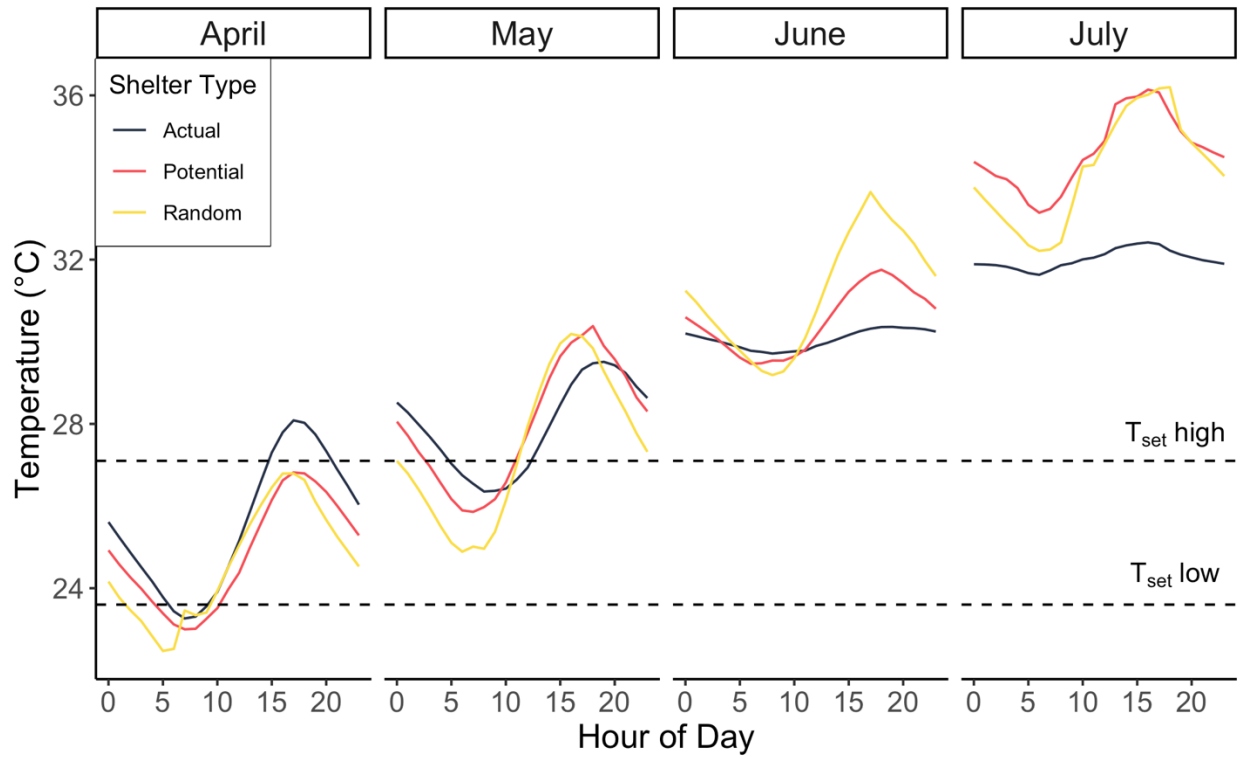


Figure 4-5. Mean hourly temperature for each shelter type by month and hour of day (n=48). The dashed lines indicate the target thermoregulatory range (lower and upper T_{set}).

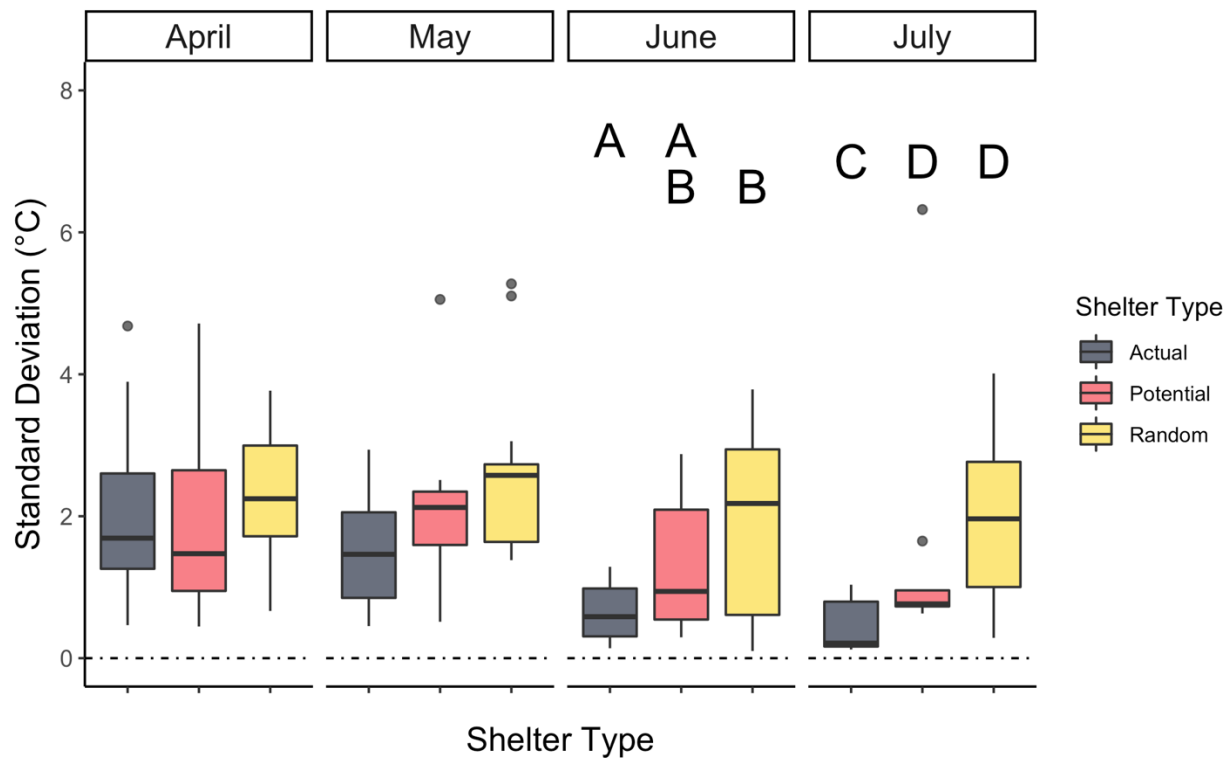


Figure 4-6. Thermal stability of shelters as measured by standard deviation from the mean temperature for each shelter type across all months (n=17 for April; n=13 for May; n=9 for June; n=9 for July). A deviation of 0°C would indicate that there is no fluctuation of temperature (noted by dashed line). 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.

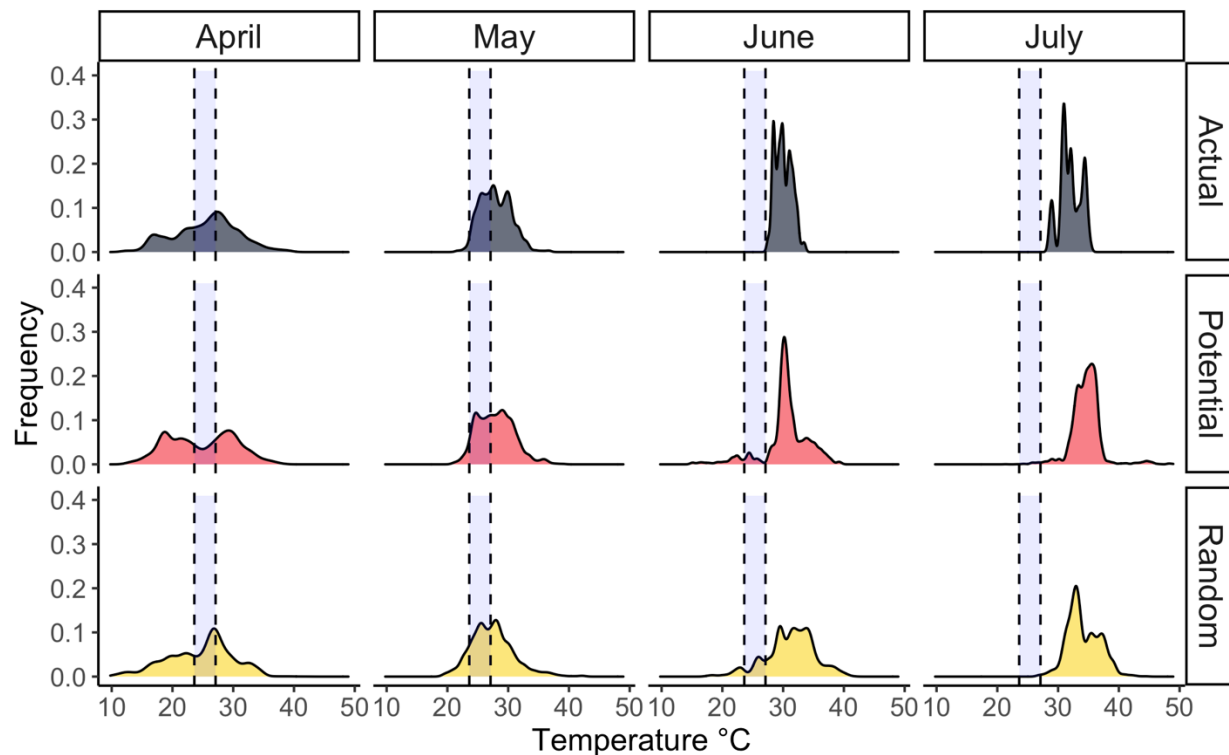


Figure 4-7. Density plot showing the frequency of temperatures recorded for each shelter type by month. (n=7,361 in April; n=5,629 in May; n=3,897 in June; n=3,897 in July). The shaded blue regions indicate the lower and upper set-point range (T_{set}).

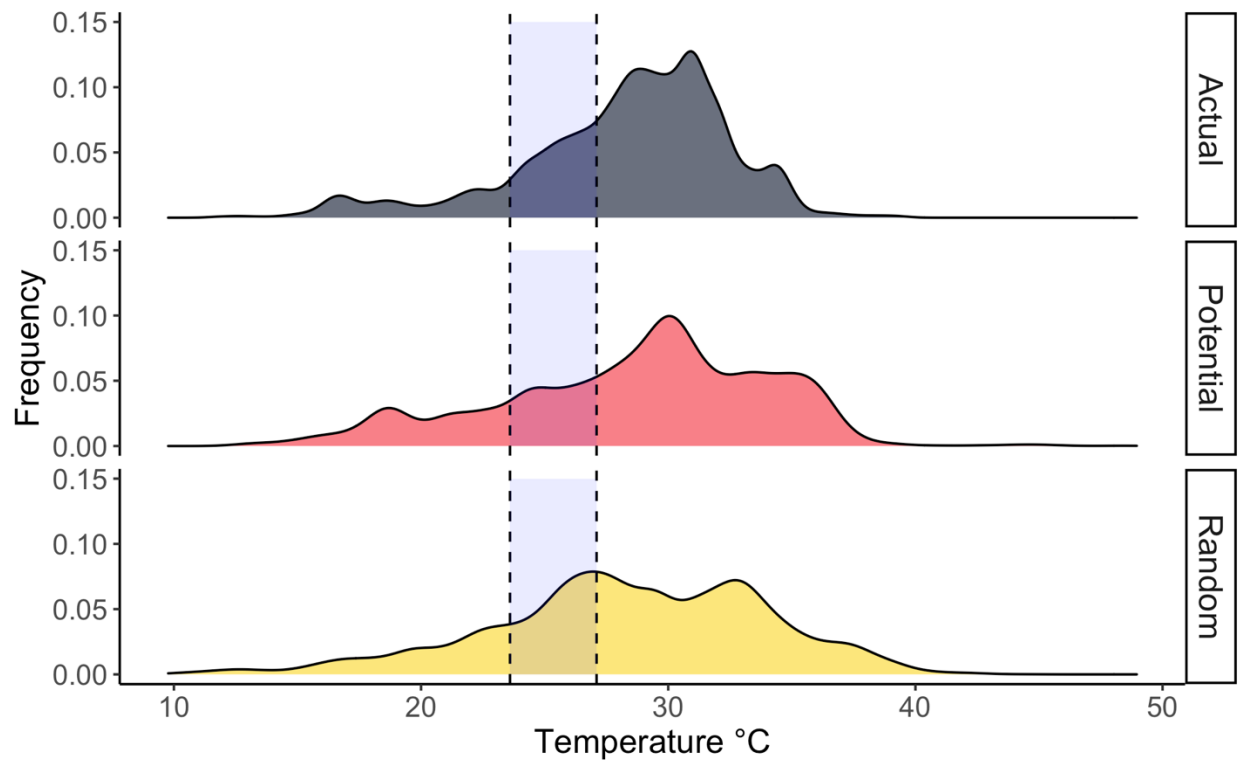


Figure 4-8. Density plot showing the frequency of all temperatures recorded for each shelter type (n=20,784 for each). The shaded blue regions indicate the lower and upper set-point range (T_{set}).

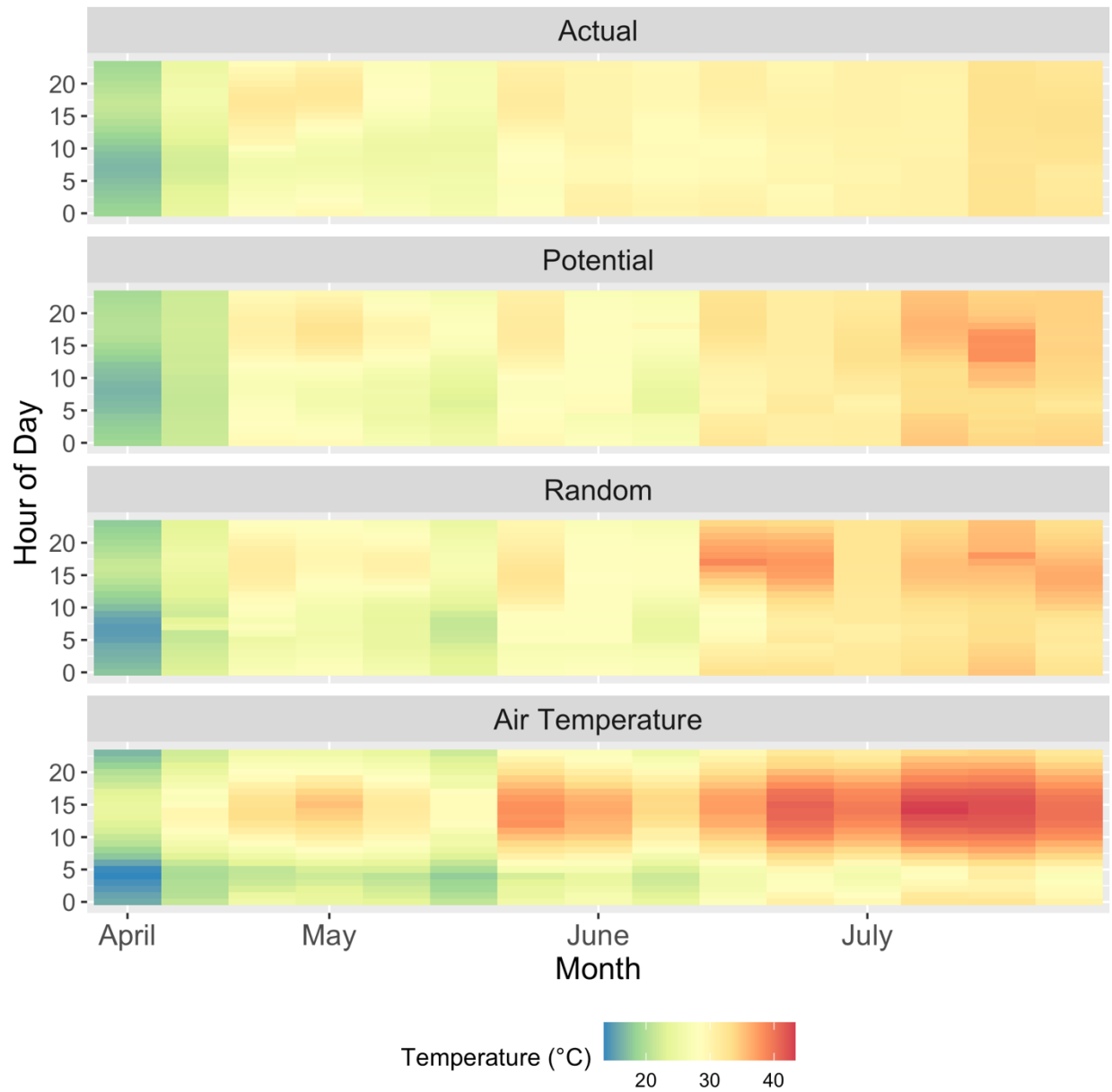


Figure 4-9. Heat map displaying the hourly means of temperatures within each shelter type and for above-ground air temperatures by week (starting second week of April).

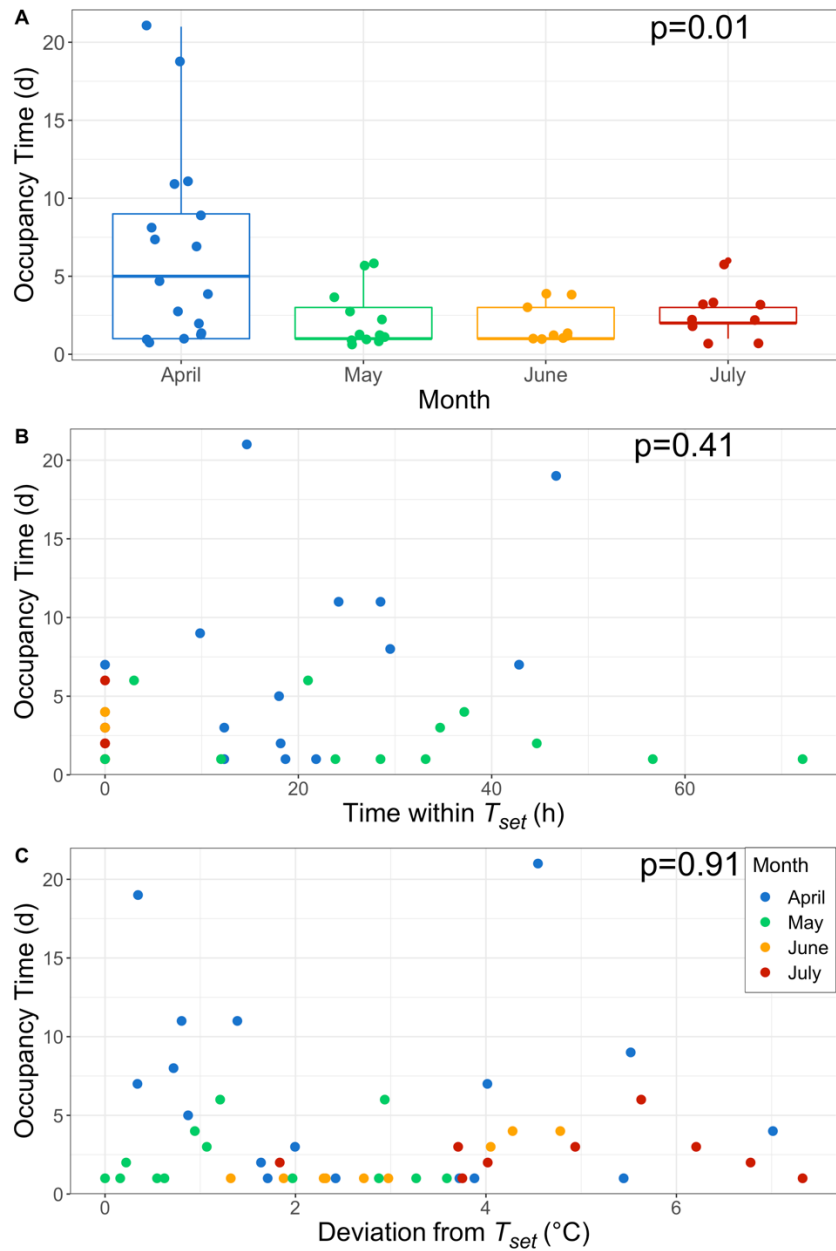


Figure 4-10. Monthly effect of thermal quality on shelter occupancy. Occupancy duration is plotted A.) against the total hours spent within the set-point range (T_{set}), B.) against the average deviation from T_{set} for each shelter and C.) by month.

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Part 5: Observation of long-term shelter re-use

In visiting previous Gila monster study sites in Clark County, we discovered a Gila monster occupying a shelter that had been used by other individuals 16 years previously. This observation was published in the journal *Herpetological Review* (published account is copied below). Although this is a single anecdotal observation, it highlights the importance that shelter sites may play in the ecology and persistence of Gila monsters in Clark County.

Gienger, C.M., S. Cohen, J. Jones, and C.R. Tracy. 2021. Refuge Reuse. *Heloderma suspectum* (Gila Monster) 52(3):648.

HELODERMA SUSPECTUM (Gila Monster). REFUGE REUSE. Gila Monsters are secretive lizards that spend most of their time in underground shelters such as caves, crevices, and burrows (Beck 2005. *Biology of Gila Monsters and Beaded Lizards*. University of California Press, Berkeley, California. 211 pp.). Shelter sites appear to be carefully selected and serve multiple functions as refuges during harsh summer conditions and for overwintering (Beck and Jennings 2003. *Herpetol. Monog.* 17:111–129). Gila Monsters show high fidelity to specific shelters, returning repeatedly to the same shelter during the active season, which they may share with other Gila Monsters, as well as with other species such as desert tortoises, rattlesnakes, skunks, and jackrabbits (Beck and Jennings 2003, *op. cit.*). Considering the importance of shelters, it would be expected that Gila Monsters would use high quality shelters for many years, but this is not well known.

We radio-tracked Gila Monsters in southern Nevada, USA, ca. 10 km from Lake Mead, from 2001–2004, measuring patterns of refuge-site selection and reuse (Gienger 2003. M.S. Thesis, University of Nevada, Reno, Nevada. 55 pp.). On 18 May 2002 we tracked an adult male Gila Monster (ID #020: 276 mm SVL, 357 g) to the opening of a crevice shelter on the side of a rocky sandstone outcrop (shelter #885). The crevice appeared to continue underground for several meters and the vestibule-like opening measured 90 cm wide by 25 cm high, faced outward at 330 degrees, and had a fine sandy substratum. On 18 May 2003 we found an adult female (ID #190: 296 mm SVL, 389 g) in the same shelter (#885) for one day; from 22–24 May 2003 a male (ID #020) had also returned to this shelter, and on 24 May the female had returned. Between 26 May and 4 June 2003 male #020 intermittently left and returned to shelter #885. No additional Gila Monsters were tracked to this shelter site until 1808 h on 24 May 2004, when ID #020 was found occupying the site for the third consecutive year, this time staying for less than 12 h. Sixteen years later, on 25 May 2020, we revisited our study site to search for Gila Monsters in previously used shelters and found a small adult Gila Monster (275 mm SVL, 340 g) in shelter #885.

Shelter #885 is an active season shelter and to our knowledge this is the longest known repeated use of a single Gila Monster shelter, although Beck and Jennings (2003, *op. cit.*) found overwintering shelter re-use for six consecutive years. Our inter-decadal observations suggest that individual shelters play an important role in the ecology of Gila Monsters, and that such sites may even be used by successive generations of individuals.

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