

HABITAT USE BY GILA MONSTERS: THE IMPORTANCE OF SHELTERS

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ABSTRACT: Many desert organisms cope with extreme and variable conditions by retreating to sub-surface refugia, yet little is known of the patterns of refuge use by most desert inhabitants. We investigated shelter use by the Gila Monster, *Heloderma suspectum*, an ectotherm closely tied to sub-surface refugia in a strongly seasonal desert environment. We addressed hypotheses that ectotherms may use habitats based on availability of shelters, select shelters based on particular cues, respond to seasonal variation in refuge characteristics, and show fidelity to specific retreats. Using radiotelemetry, we monitored microhabitat use by eight to ten Gila Monsters for six years, recording timing, frequency, and duration of visitation to over 250 specific shelters. We used transects to assess shelter availability, recorded structural features of all shelters, and used dataloggers to monitor seasonal changes in microenvironments within subsets of shelters for periods up to two years. Shelters, and the habitats where they occurred, were not chosen by Gila Monsters at random. *Heloderma* spent more time in areas where a higher density of potential shelters was available, and selected shelters based on rockiness, slope and entrance aspect, depth, humidity, and temperature. Gila Monsters showed longer residence times and greater fidelity to shelters used during extreme periods (e.g., winter) and these patterns were paralleled by seasonal changes in the characteristics of shelters chosen. Winter shelters tended to be south-facing, rockier, deeper, and warmer than those used in other seasons, whereas dry-summer shelters were more soil-like in composition, cooler, and more humid. Gila Monsters showed strong fidelity to specific shelters, some of which were used by two or more lizards, sometimes concurrently. Seasonal variation in use of "social" shelters coincided with annual cycles of intraspecific behaviors and reproduction. Our results underscore the importance of sub-surface refugia in the ecology of a sedentary desert ectotherm. Because many other ectotherms also spend significant periods sequestered in below-ground retreats, it is surprising that ecologists have not more extensively investigated this phenomenon. An understanding of the cues used by desert ectotherms to choose refuge-sites, the spatial and temporal variability in refuge characteristics, and the fidelity shown to particular retreats, may help better explain patterns of habitat selection, behavior, distribution, and abundance.

Key words: Desert; Gila Monster; Habitat; Habitat selection; *Heloderma*; Humidity; Microenvironment; Microhabitat; Refugia; Shelter-site; Temperature.

INTRODUCTION

Most small terrestrial animals are closely tied to sub-surface refugia, or shelters. Desert scorpions (Polis et al., 1886), beetles (Rasa, 1995), spiders (Henschel, 1998; Humphreys, 1978), mammals (Buffenstein, 1984; Schmidt-Nielson, 1964; Randall, 1993; Tracy and Walsberg, 2002), and reptiles (Bulova, 1994; Huey et al., 1989; Norris, 1953; Pough et al., 1978; Zimmerman et al., 1994) all cope with harsh environmental conditions and wide fluctuations in availability of resources by exploiting a more benign environment within shelters. Many ectotherms spend far more time sequestered in below-ground refugia than they do above ground (Avery, 1976; Beck,

1990; Huey, 1982; Huey et al., 1989; Nagy and Medica, 1986; Polis et al., 1986). For animals such as these, shelters provide escape from extreme surface temperatures and from predators, and allow access to favorable thermoregulatory sites, foraging areas, and potential mates (Blazquez and Rodriguez-Estrella, 2001; Bulova, 1994; Christian et al., 1983; 1984; Downes and Shine, 1998; Humphreys, 1978; Schlesinger and Shine, 1994; Zimmerman et al., 1994). Shelters are particularly important for ectotherms because their body temperatures, and associated resting metabolic rates, are determined by the microenvironment within such refugia (Christian et al., 1995; Huey, 1991; Zimmerman et al., 1994). The appropriate choice of a refuge, therefore, has profound implications for the ecology of desert animals. Indeed, retreat to refugia is

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arguably the most common and important way that small desert animals persist in harsh and variable environments.

Some desert animals, including species of reptiles (Heatwole, 1977; Pianka, 1966), mammals (Nevo et al., 1979; Price, 1978), and arthropods (Krasnov and Shenbrot, 1996; Polis et al., 1986), may select habitats based on structural microhabitat features, such as availability and quality of subsurface refugia. Population densities of desert rodents are influenced by factors affecting the availability of burrows (Feldhamer, 1979), and kangaroo rat burrows, in turn, influence the abundance and diversity of ground-dwelling ectotherms (Hawkins and Nicoletto, 1992). Despite the obvious importance of shelters in the ecology of organisms inhabiting harsh or seasonal environments, very little is known about refuge use by most desert ectotherms, cues used to choose shelters, fidelity to refuge sites, and the degree to which shelter availability and quality influences habitat use and local dispersion.

We investigated habitat use by a large, sedentary desert lizard, the Gila Monster (*Heloderma suspectum* Cope). We used radio-telemetry to determine how this desert ectotherm may respond to spatial and temporal variation in the availability and quality of refuge sites. In addition, we assessed the fidelity shown by Gila Monsters to particular retreat sites and explored potential roles such refugia play in the ecology of this and other sedentary desert ectotherms.

We address the following hypotheses and predictions: 1) Habitat use is influenced by shelter availability and shelter "quality". If so, we predicted Gila Monsters would spend more time in habitats harboring a higher density of potential shelters, and in habitats possessing shelters with certain attributes. 2) Shelters are selected based on certain physical and micro-environmental attributes. If this were true, we predicted shelters used by Gila Monsters would differ in specific structural characteristics (such as depth, rockiness, and entrance aspect) and microenvironmental features (e.g., temperature and vapor pressure) from potential shelters that were not used. 3) Characteristics of shelters chosen by Gila Monsters vary in relation to seasonal changes of microenvironments within shelters, and shelter microenvironments are influenced by physical

characteristics of shelters such as depth, rockiness, and entrance aspect. We predicted that if seasonal changes in shelter microhabitats were important, Gila Monsters would select shelters with different characteristics during different seasons, and that structural traits of shelters would be correlated with microenvironments therein. 4) Gila Monsters show strong fidelity to particular retreat sites. If this were true, we predicted a high proportion of shelters would be revisited by Gila Monsters and that re-used shelters might show characteristics that set them apart from others. We also predicted that shelter re-use may vary seasonally. We attempt to integrate our results into a fuller understanding of the importance of shelters in the ecology of this and other desert organisms.

Gila Monsters are excellent subjects for investigating patterns of refuge use because many aspects of their ecology tie them to shelters (Plate 1). They are nest predators, feeding upon juvenile mammals and eggs of ground nesting birds and reptiles (Beck, 1990; Bogert and Martín del Campo, 1956; Lowe et al., 1986). Although finding such prey requires considerable searching, helodermatid lizards spend the vast majority (95–98%) of their time at rest in shelters (Beck, 1990; Beck and Lowe, 1991; Porzer, 1981). Gila Monsters have very low resting metabolic rates (Beck and Lowe, 1994), can consume large meals (>33% of adult body mass; Beck, 1990; Lowe et al., 1986), and store fat within the body cavity and tail (Bogert and Martín del Campo, 1956). These traits make frequent foraging unnecessary. When on the surface, Gila Monsters are particularly vulnerable to predators because, unlike most other lizards, they are unable to escape by quickly sprinting away (Beck et al., 1995), but rely instead on a painful, venomous bite (Bogert and Martín del Campo, 1956). Shelters may, therefore, be important as refugia from potential predators.

In addition, shelters may serve as refugia from harsh environmental conditions on the surface. Gila Monsters show a peak in annual activity during May, a hot and very dry period throughout their range (Beck, 1990; Beck and Lowe, 1991; Lowe et al., 1986) yet they also prefer relatively low body temperatures (28–30 C) while active or basking (Beck, 1990; Porzer, 1981). They become physiologically



PLATE 1.—Gila Monsters inhabit hot desert regions of North America and show a peak in activity during the driest time of year. Refuge offered by shelter sites, as shown here, is the primary means by which these lizards, and other ectotherms, cope with harsh seasonal environments of deserts.

stressed at body temperatures approaching 38 C (Bogert and Martín del Campo, 1956). Interestingly, helodermatid lizards also show rates of water loss that appear unusually high

for desert lizards (Lowe et al., 1986; Porter and Beck, unpublished data), a trait that may be better understood given their evolutionary origins in more mesic environments (Pregill

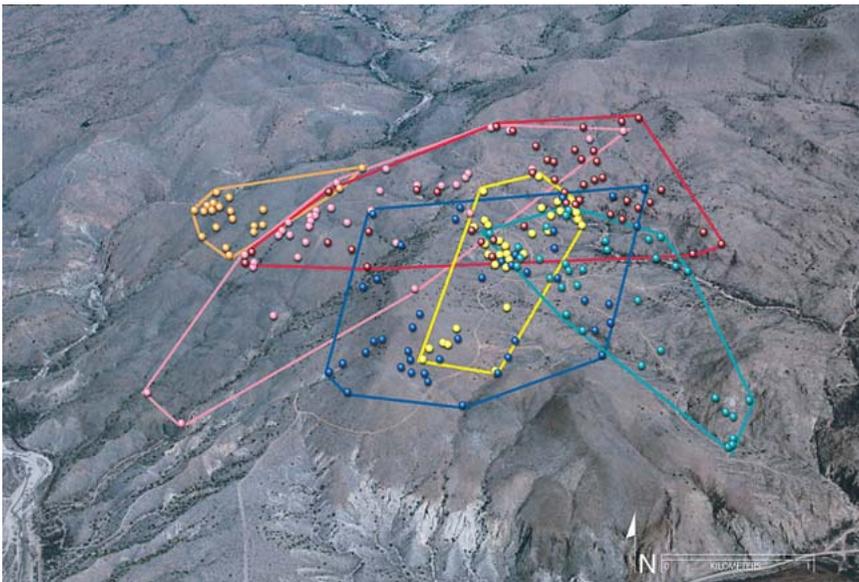


PLATE 2.—Shelter-site locations (dots) used by six Gila Monsters radiotracked from April to July 1992, and monitored at least weekly from November 1992 through June 1994. Each color denotes an individual Gila Monster (red = male no. 1; yellow = female no. 2; green = male no. 5; blue = male no. 8; orange = female no. 9; and pink = female no. 10). Minimum convex polygon home ranges are indicated by solid lines (see also Table 5). Not all lizards monitored in this study are shown on this photograph.

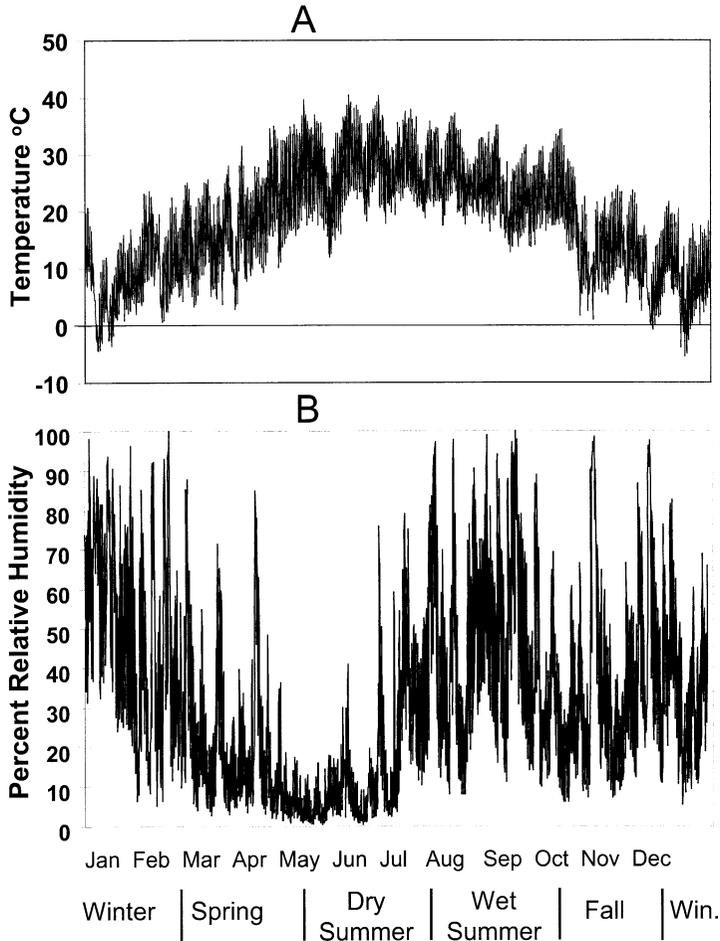


FIG. 1.—Variation in ambient temperature (A) and relative humidity (B) over a typical one-year period on the Red Rock study site.

et al., 1986; Stevens, 1977). Potentially high rates of water loss while Gila Monsters are active during the dry season may make shelters important not only for escaping the heat, but also for reducing desiccation.

METHODS

Site Description

Our study area is a Chihuahuan semidesert grassland (Brown, 1982) in southwestern New Mexico at 32° 44.5' N latitude and 108° 42.0' W longitude, 5 km NW of Red Rock, Grant County. Topography ranges from 1250 to 1500 m in elevation and consists of rocky slopes and small dry canyons along the Gila River. Dominant vegetation consists of catclaw (*Acacia greggi*, *Mimosa biuncifera*), snakeweed

(*Gutierrezia* sp.), ocotillo (*Fouquieria splendens*), mesquite (*Prosopis juliflora*), creosote-bush (*Larrea tridentata*), juniper (*Juniperus monosperma*), cacti (*Opuntia* spp.), sotol (*Dasylirion wheeleri*), and grasses. Predominant rocks are strongly weathered Precambrian granites of the Burro Mountain batholith (Hewitt, 1959). Annual precipitation averages 363 mm, with 60% falling from July through October (Red Rock weather station, averaging period = 1971–1993). Temperature variation can be extreme, with air temperatures commonly exceeding 40 C in summer and dropping below 0 C in winter (Fig. 1A). Relative humidity also varies greatly, with daily means below 5% during dry summer periods and over 50% during some wet summer and winter periods (Fig. 1B). These

patterns of temperature, precipitation, and relative humidity result in five distinct seasons at our study site: Winter (December through February), Spring (March through mid-May), Dry Summer (mid-May through mid-July), Wet Summer (with the onset of the summer rains, mid-July through September) and Fall (October–November; Fig. 1).

General Study Procedures

We focused on Gila Monsters encountered within a 4.5 km² core area near a perennial spring. Between April 1992 and December 1998, eight adult Gila Monsters (four males and four females) were outfitted with implantable, temperature-sensing radiotransmitters (Model IMP-150, Telonics Telemetry, Mesa, AZ). Two more lizards were outfitted with radiotransmitters in 2000 to conduct experiments on shelter selection (see below). Transmitters were surgically implanted using the techniques of Beck (1990). Size, sex, and reproductive condition were recorded for each lizard; movements and shelter use were monitored with a directional antenna and a TR-2 or TR-4 receiver (Telonics). From May 1992 to July 1994, we closely monitored activity patterns and shelter use by these lizards (three or more times/wk during the activity season; once/wk during the winter); more than 200 shelters were marked and characterized. During this two year period, we identified areas showing high use and low use (defined below) by Gila Monsters within the core area of the study site. From August 1994 to December 1998 we monitored shelter use by these lizards less frequently (weekly to monthly), characterized additional shelters observed, and gathered microhabitat data necessary to address the hypotheses outlined above.

Throughout the study we marked shelters with small rock cairns and tagged them for future identification. We marked locations of shelters on maps drawn from aerial photographs, and calculated home ranges using the minimum convex polygon method (Jennrich and Turner, 1969; Rose, 1982). We recorded the following characteristics: height and width of shelter entrance, depth (accurate up to about 1 m, after which shelter depth was estimated using transmitter signal), aspect of entrance and slope on which shelter occurred,

and rockiness of shelter. To index shelter rockiness, we used an ordinal scale ranging from 1 to 5 (1 = silt-sand, 2 = sand/gravel, 3 = gravel, 4 = gravel/rock, 5 = rock) for both the roof and the floor of the shelter. Whenever possible, we recorded the number of days each Gila Monster spent in each shelter. A few shelters were not completely characterized; shelters for which we were unable to determine specific characteristics (e.g., depth, duration of residency) were not included in analyses, therefore sample sizes vary slightly among analyses.

Hypothesis 1: Is Habitat Use Influenced by Shelter Availability and Shelter Quality?

To understand the role of shelter availability in habitat use by Gila Monsters, we set up 20 100 m × 2 m transects, 10 in high-use and 10 in low-use areas, and identified all potential shelters along the transects. We defined low-use areas as portions of our study site that were obviously accessible to Gila Monsters (i.e., within home ranges of lizards we monitored), but that showed < two visit/ha by lizards we followed with radiotelemetry during the first 2 yr of our study (1992–1994; see Plate 2). “High-use” areas received more than two visits/ha during the same period. We defined a “potential shelter” as a stable hole or crevice at least 5 cm in diameter and 20 cm deep, the dimensions of the smallest shelter observed to harbor a Gila Monster. We tested for differences in the number of potential shelters between high- and low-use areas using the Mann-Whitney test. If habitat use were not influenced by shelter availability, we expected to see no difference in potential shelter abundance between high-use and low-use areas.

To determine whether the quality of potential shelters influenced habitats used by Gila Monsters, we compared features of 28 potential shelters in low-use areas with those of 35 potential shelters in high-use areas. Potential shelters were located by haphazardly searching regions of the study area. Because some shelter characteristics were continuous variables (i.e., entrance dimensions and shelter depth), and others were discrete (roof and floor rockiness, aspect), and because not all variables satisfied parametric assumptions of normality, we employed a class of nonpara-

metric statistics using ranked data to test this and other hypotheses (Conover, 1980; Conover and Iman, 1981). In this case, characteristics of potential shelters (except aspect) were ranked and subjected to a one-way analysis of variance (PROC RANK and PROC GLM, SAS Inst, 1985) to test the hypothesis of no mean ranked difference between shelters in high-use and low-use areas. To test hypotheses relating to shelter and slope aspect, we grouped observations into one of eight directional categories (N, NE, E, SE, S, SW, W, NW) and used G-tests (with Williams correction, Sokal and Rohlf, 1995). If habitat use was not influenced by the quality of potential shelters, we expected no differences in potential shelter characteristics between high-use and low-use areas.

Hypothesis 2: Shelter Selection

To address whether Gila Monsters selected shelters based on certain attributes, we compared the physical characteristics of “actual shelters” in high-use areas with “potential neighboring shelters” not known to be used by a Gila Monster. We defined an “actual shelter” as a shelter observed to have been used by a Gila Monster for at least several hours and we treated each shelter used by a Gila Monster as an independent sample. A sample of 48 such shelters used by seven radio-equipped lizards was haphazardly chosen from throughout the study area. To reduce biases associated with microhabitat, aspect, and substrate type, we paired each actual shelter with a potential neighboring shelter by walking an ever-increasing spiral with the actual shelter at its vortex until a potential shelter (fulfilling potential shelter criteria as described above) was encountered. We assumed that potential shelters were unused because we never observed any to be inhabited by a Gila Monster over the 6 yr they were monitored, although a possibility always existed that their use went undetected. Differences in structural characteristics (described above) between actual vs. potential shelter pairs were compared using the Wilcoxon paired-sample *t*-tests (PROC MEANS, SAS Inst., 1985). To eliminate biases associated with treating each shelter (rather than each lizard) as an independent sample (and to avoid pseudoreplication), we used degrees of freedom based on

the number of Gila Monsters (7) selecting actual shelters rather than the number of shelter pairs (48).

To explore the role of microenvironment (temperature and vapor pressure deficit) in shelter selection, we monitored an additional 17 pairs of actual vs. potential neighboring shelters used by five Gila Monsters during the activity season between 28 April and 10 June 2000. For each pair, a datalogger was placed 0.4 to 1.0 m deep within an actual shelter inhabited by a Gila Monster, and a second datalogger placed (at the same depth) in the nearest potential neighboring shelter that matched the inhabited shelter in diameter, rockiness, and aspect. We simultaneously recorded temperature and humidity in each pair of shelters using Hobo™ XT and Rh dataloggers (see below) for a minimum of 48 h during and after occupancy. Vapor pressure deficit (in kilopascals, kPa) was calculated from datalogger measurements of temperature and relative humidity. Temperature and vapor pressure deficit, during and after occupation, were ranked and compared between the 17 actual and potential pairs using a blocked three-way ANOVA (PROC RANK and PROC GLM, SAS Inst, 1985). Individual lizards were blocked in the analysis to eliminate potential biases and to avoid pseudoreplication (Heffner et al., 1996; Hurlbert, 1984). Whether a shelter was used by a Gila Monster or not (actual vs. potential shelters) and periods of occupancy (current vs. post-occupancy) were used as main effects. Interactions among main effects were also evaluated. We compared periods of post-occupancy with current occupancy to control for possible changes in shelter microenvironment, especially vapor pressure deficit (due to evaporative water loss), brought about by the presence of a Gila Monster within the shelter. If microenvironment were not a factor in shelter selection by Gila Monsters, we would expect to see no differences between actual and potential shelters in internal temperature or vapor pressure deficit.

Hypothesis 3: Seasonal Effects

Based on observations from 1992–1994, we use the term “shelter type” to differentiate shelters used in each of three focal seasons: “Winter”, when shelters presumably serve as refugia from low temperature, “Dry Summer”,

when shelters serve as refugia from high surface temperatures and high vapor pressure deficit, and "Spring" when shelters serve more as temporary refugia between foraging bouts and as potential mating sites.

To assess whether structural attributes of shelters chosen by Gila Monsters differed among seasons, we used Kruskal-Wallis tests (PROC RANK and PROC GLM, SAS Inst., 1985) with ranked shelter characteristics (except aspect) as dependent variables and season of use (i.e., shelter type) as the class variable. To test hypotheses relating to shelter and slope orientation, we grouped observations into one of eight directional categories (N, NE, E, SE, S, SW, W, NW) and used G-tests (with Williams correction, Sokal and Rohlf, 1995).

To explore seasonal differences in microenvironments among shelter types, we monitored temperature and vapor pressure deficit within actual Gila Monster shelters between January 1995 and August 1996. We pre-set Hobo™ XT and Rh dataloggers (4.5 × 4.5 × 1.5 cm; Onset Instruments, Inc.) to record temperature and relative humidity every 72 min and placed them up to 1 m deep within shelters. Vapor pressure deficit (kPa) was calculated using relative humidity and temperature. Shelters were unoccupied by Gila Monsters while the dataloggers were in place. We attempted to place dataloggers at depths within shelters similar to those chosen by Gila Monsters (based on our observations from monitoring radio-implanted lizards) to assess the microenvironment experienced by a hypothetical lizard inhabiting that particular shelter (Vitt and Sartorius 1999).

We monitored microenvironments within a total of 27 shelters: 9 "Winter" shelters, 9 "Dry Summer" shelters and, 9 "Spring" shelters. To test for differences in microenvironments among these three shelter types, we subjected ranked temperature and vapor pressure deficit to a blocked, two-way, nested analysis of covariance (PROC RANK and PROC GLM, SAS Inst., 1985). Temperature and relative humidity were sampled for one to four-week periods between January 1995 and August 1996. During a given sampling period, 3 shelters of each of the 3 shelter types (a total of nine shelters at any one time) were monitored with a temperature and a humidity

datalogger. Temperature and vapor pressure deficit data were ranked and then averaged for each sampling period. Sampling periods were nested within season (Winter, Spring, Dry summer, and Wet summer/Fall) and individual shelters were nested within shelter type (Winter, Dry summer, and Spring). The ranked depth at which dataloggers were positioned within the shelter was used as a co-variate within the overall analysis. Post-hoc ($\alpha = 0.05$) differences in microenvironments among seasons and shelter types were assessed using pairwise comparisons of least squares means. If Gila Monsters did not select shelters with different microenvironmental attributes during different seasons, we would expect to see no differences in shelter microenvironment across seasons.

To assess the potential influence of shelter attributes on shelter microenvironment, we performed stepwise multiple regressions (with maxr option) by season (PROC STEPWISE, SAS Inst., 1985). Because temperature and vapor pressure deficit were regressed against ordinal data (roof and floor substrate), all variables used in the analysis were ranked (PROC RANK, SAS Inst., 1985). Ranks of temperature and vapor pressure deficit, in turn, were used as dependent variables. Ranks of four shelter attributes: rockiness of the roof and floor, aspect, and depth, were used as independent variables. Using this approach, we determined which of the four physical aspects of shelters were best predictors of microenvironment.

Hypothesis 4: Shelter Fidelity

To determine the extent to which shelters were revisited, seasonal effects on shelter fidelity, and whether revisited shelters differed from those not observed to be reused, we recorded the number of times individual shelters were revisited (and by how many lizards), the proportion of total shelters that were revisited throughout each year (and season), and, whenever possible, the Gila Monster's duration of residency within each shelter. To eliminate the potential for pseudoreplication, individual lizards, not shelters, were sample units in all statistical tests; sample sizes and degrees of freedom were adjusted accordingly. Tests for mean rank differences between reused and other shelters were

conducted using the Kruskal-Wallis test (PROC MEANS, PROC RANK and PROC GLM, SAS Inst., 1985) and the Mann-Whitney test. Seasonal effects upon duration of residency (d) were assessed using the Kruskal-Wallis test. To test for seasonal effects on frequency of shelter reuse, and for differences in entrance aspect between reused and other shelters, we used G-tests (with Williams correction, Sokal and Rohlf, 1995).

RESULTS

Habitat Use, Shelter Availability, and Shelter Quality

We characterized and monitored 259 shelters used by 10 Gila Monsters on the study site. The spatial relationships among most shelters used by 6 of those lizards are shown in Plate 2. Home range sizes varied greatly, from 6.2 ha to 104.8 ha (mean = 58.1, SE = 12.4, see plate 2). Although Gila Monsters generally used pre-existing cavities as shelters, we occasionally observed them modify shelters, especially soil burrows, by digging. High use areas (>2 visits/ha) had more potential shelters (mean = 3.5 potential shelters per transect, SD = 2.59) than low use areas (mean = 0.2 potential shelters per transect, SD = 0.42; Mann-Whitney $U = 94$, $n_1 = 10$, $n_2 = 10$, $P < 0.05$). High use areas harbored potential shelters with significantly rockier roof structure (median = 5 [rocky]) than potential shelters found in low use areas (median = 1.5 [soil/gravel]; $F_{1,62} = 16.0$, $P = 0.0001$). Potential shelter entrances and slope aspects in high use areas were significantly more strongly oriented toward the southeast and southwest than were those in low-use areas ($G_{Williams} = 17.7$, $P = 0.013$; and $G_{Williams} = 13.76$, $P = 0.033$ for entrance aspect and slope aspect, respectively; Fig. 2).

Shelter Selection

We found actual shelters were significantly deeper (mean = 55.0 cm, SD = 37.04) than nearest potential unused neighboring shelters (mean = 39.3 cm, SD = 25.92; $t = 3.89$, $df = 6$, $P = 0.009$). We detected no differences between actual and potential neighboring shelters in other physical characteristics tested. Actual shelters selected during the activity season (April–June) had a significantly

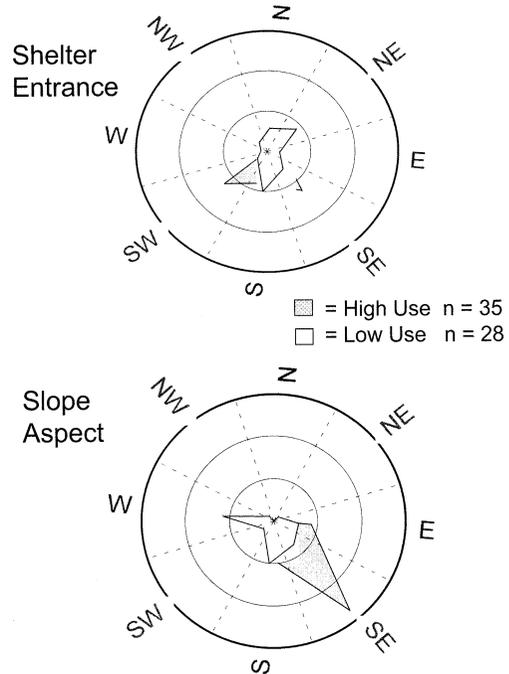


FIG. 2.—Plots of the aspect of potential shelter entrances, and slopes on which they occurred (percent of sample falling in each of eight directions). Aspect differed significantly between high-use areas (>2 visits/ha/2 yr) and low-use areas (<2 visits/ha/2 yr). Each concentric circle represents 25% of the sample.

smaller rank mean vapor pressure deficit (mean = 0.253 kPa, SE = 0.008) than potential neighboring shelters (mean = 0.308 kPa, SE = 0.008), even after variance explained by differences among lizards was removed from the model ($F_{1,60} = 9.81$, $P = 0.0027$; Fig. 3). No differences in rank mean temperature were detected for those same shelter pairs (Fig. 3). Shelters did not differ in rank mean vapor pressure deficit nor in rank mean temperature between current occupancy and post-occupancy periods, nor were there any significant interactions between the main effects.

Seasonal Effects

Many characteristics of shelters used by Gila Monsters varied significantly across seasons. Shelters used during the winter, fall, and dry summer were deeper than those selected during the wet summer and spring ($F_{4,169} = 15.43$, $P = 0.001$; Table 1). Shelters differed significantly across seasons in both roof

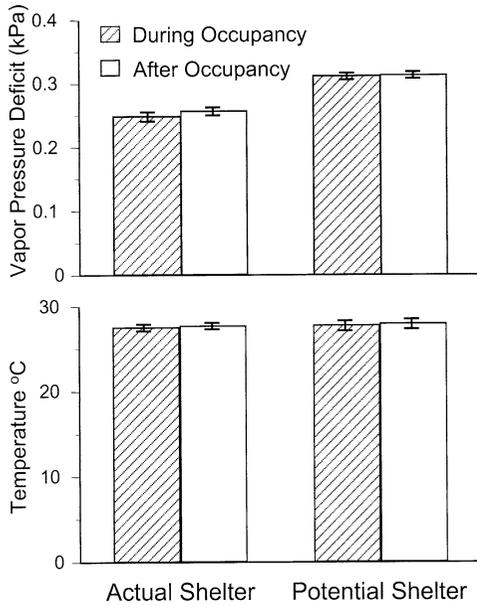


FIG. 3.—Comparison of temperature and vapor pressure deficit from 17 Gila Monster shelters paired with similar potential neighboring (but unused) shelters monitored for 48 h (during and after occupancy) during the activity season. Values reported are means \pm one standard error (horizontal bars).

($F_{4,240} = 6.53$, $P = 0.0001$) and floor ($F_{4,240} = 4.07$, $P = 0.003$) substrate, with winter shelters being rockier, and dry-summer shelters being composed of more gravel and soil (Table 1). Entrance aspect also differed significantly among shelters used in different seasons ($G_{\text{Williams}} = 47.3$, $df = 28$, $P < 0.025$). Fall and winter shelters occurred on south-facing slopes with entrances also oriented toward the south; a preponderance of spring shelter entrances faced east; and summer shelters were more variable in orientation (Fig. 4). Gila Monsters had longer residence times in shelters in the winter and fall, and switched shelters more frequently during

spring and summer (Kruskal-Wallis $H = 36.68$, $df = 4$, $P < 0.001$, Table 2).

As expected, rank mean temperature within Gila Monster shelters differed significantly throughout the year ($F_{3,20} = 36.35$, $P = 0.0001$; Table 3). Rank mean vapor pressure deficit did not differ across seasons, although it did differ among sampling periods within seasons ($F_{20,148} = 2.42$, $P = 0.001$). Independent of seasonal or sampling period variation, mean rank temperature and vapor pressure deficit also differed among shelter types (Fig. 5). The dry-summer shelters were significantly cooler throughout the year than winter and spring shelters ($F_{2,161} = 25.95$, $P = 0.0001$; Fig 5A). Dry-summer shelters also exhibited the smallest mean rank vapor pressure deficit during the year, which was significantly smaller than that of spring shelters ($F_{2,148} = 3.31$, $P = 0.039$). Winter shelters exhibited intermediate rank vapor pressure deficits (Fig. 5B). Within seasons there were also significant differences in temperature and vapor pressure deficit among shelter types (based on post-hoc pairwise comparisons of least squares means, $P < 0.05$). Dry-summer refugia were generally cooler and more humid than other shelter types, while winter refugia were significantly warmer during winter (Fig. 5A and B).

Two structural features of shelters significantly predicted shelter microenvironment (Table 4). Roof rockiness exhibited positive partial regression coefficients with temperature (during fall, wet summer, dry summer and winter) and vapor pressure deficit (dry summer; Table 4). The addition of other independent variables provided no significant increment to R^2 or possessed significant predictive power. Based on these analyses, rocky shelters were generally warmer and drier during the indicated seasons than soil-like shelters. During the dry summer, shelter

TABLE 1.—Seasonal variation in structural traits of shelters used by Gila Monsters. Roof and floor substrates were scored from 1 (silt/sand) to 5 (rock), as described in text. Values are mean substrate scores \pm one standard error; those with the same superscript did not differ significantly.

	Spring	Dry summer	Wet summer	Fall	Winter
Depth (cm)	49.4 \pm 6.35 ¹	89.5 \pm 6.29 ²	52.1 \pm 8.98 ¹	110.7 \pm 11.66 ^{2,3}	128.0 \pm 9.95 ³
n	54	55	27	16	22
Roof structure	4.5 \pm 0.18 ^{2,3}	3.6 \pm 0.16 ¹	3.9 \pm 0.23 ^{1,2}	4.3 \pm 0.33 ^{1,2,3}	5.0 \pm 0.29 ³
Floor structure	3.0 \pm 0.16 ¹	2.7 \pm 0.14 ¹	2.9 \pm 0.21 ¹	2.5 \pm 0.29 ¹	3.7 \pm 0.26 ²
n	68	90	41	20	26

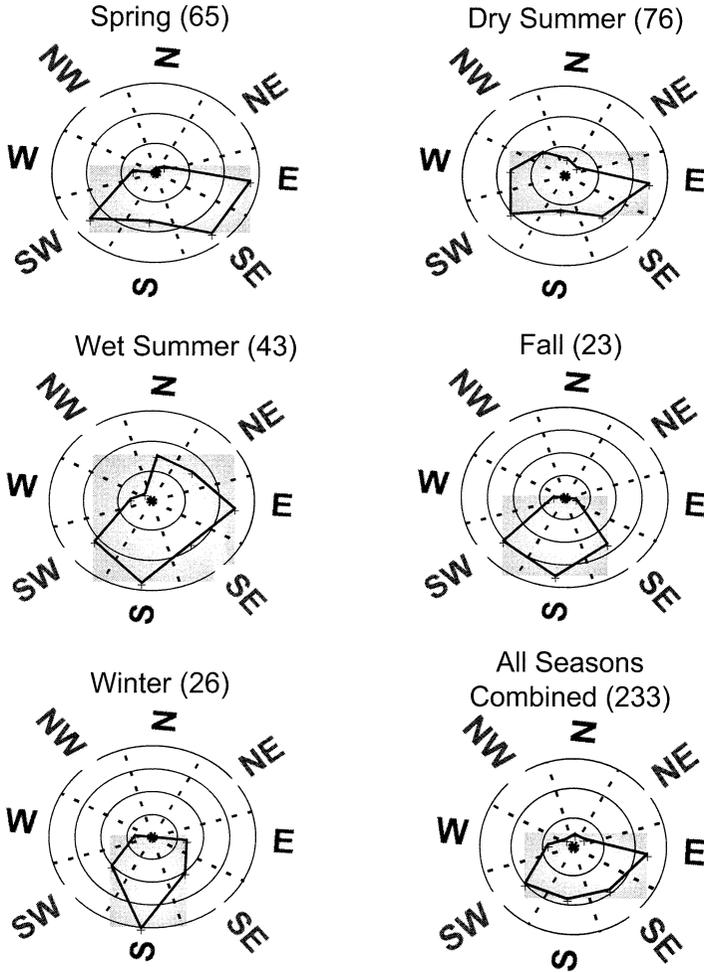


FIG. 4.—Seasonal patterns in the aspect of Gila Monster shelter entrances, expressed as percent of sample size falling in each of eight directions. Each concentric circle represents 10% of the sample. Numbers in parentheses are sample sizes.

depth exhibited a negative partial regression coefficient with temperature (the deeper the shelter the cooler). Collectively, these results indicate that physical aspects of shelters significantly predicted shelter microenvironment (Table 4).

Shelter Fidelity

Individual Gila Monsters varied considerably in the extent to which they reused shelters, ranging from 23% to 54% (mean = 42.9%, SD = 11.4, $n = 7$, based on per cent of total shelters used by each lizard; Table 5). The degree that shelters were re-used was clearly a function of duration of monitoring; an increasingly larger proportion of shelters was

reused by Gila Monsters as the study progressed (Fig. 6). Shelters repeatedly used by individual Gila Monsters had significantly rockier roofs (mean = 4.4 = rock, SE = 0.29) than shelters that were used once (mean = 3.6 = gravel/rock, SE = 0.27; $F_{1,15} = 4.54$, $P = 0.05$), but were otherwise similar in structure and aspect to shelters not observed to be reused. Gila Monsters resided significantly longer in re-used shelters (mean = 34.8 d/shelter, SE = 7.37) than in other shelters (mean = 4.4 d/shelter, SE = 0.56; Wilcoxon $W = 28$, $n = 7$, $P = 0.02$; Fig. 7). Shelter reuse also was strongly influenced by season ($G = 20.5$, $df = 4$, $P < 0.005$; Fig. 8). A larger number of shelters was reused during the dry

TABLE 2.—Seasonal patterns of shelter occupancy by Gila Monsters on the study site between November 1992 and July 1994. Values shown are means \pm one standard error; those with the same superscript did not differ significantly.

	Spring ²	Dry ² summer	Wet ² summer	Fall ¹	Winter ¹
<i>n</i>	48	43	24	22	9
Days in same shelter	5.1 \pm 1.00	4.5 \pm 1.08	4.2 \pm 0.77	13.6 \pm 2.46	88.7 \pm 1.21

summer (41 of 101 = 40.6%), but a greater proportion of shelters was reused during the winter (16 of 22 = 72.7%, Fig. 8).

Of 94 shelters that were reused, 44 (47%) were used by more than one individual ("social shelters", Fig. 9A). Twenty-four of these (54.5%) were used by two or more lizards concurrently, most commonly during the late spring and early dry-summer (Fig. 9B) mating season, when we also observed males and females together in shelters. Social shelters also differed from individual shelters in their spatial arrangement. The majority of social shelters was located near the core of our study site where lizard home ranges overlapped, whereas the majority of shelters reused by individual lizards were overwintering refugia located near the edges of home ranges. Some shelters that were used as winter refugia, however, were also reused during the dry summer.

DISCUSSION

Habitat Use, Shelter Availability, and Shelter Quality

Gila Monsters spent more time in areas where a higher density of potential shelters was available, where potential shelters tended to be rockier, and where slopes and shelter entrances were oriented more to the south. Together, these results suggest Gila Monsters selected areas of the study site based on the availability and quality of potential shelter sites. They also suggest that the availability of suitable refugia played a role in habitat selection by *Heloderma* and, in turn, influenced their patterns of local dispersion. Other terrestrial vertebrates and macroinvertebrates in arid regions also show dispersion patterns that are strongly influenced by the availability of shelters and appropriate soils in which suitable refugia may be constructed (Kinlaw, 1999; Polis et al., 1986).

Shelter Selection

Our results underscore the importance of moisture as a factor in microhabitat selection by Gila Monsters. Comparisons between actual vs. potential shelters in our study revealed that vapor pressure deficit, not temperature, significantly influenced shelter selection during the peak activity season. Humidity was also shown to influence activity patterns in a pit viper inhabiting a seasonal tropical environment (Daltry et al., 1998). When stressed by lack of water, Desert Tortoises retreat into burrows (Ruby et al., 1994) and when sleeping or dormant, their water loss rates are reduced (Wilson et al., 2001). The consequences of microhabitat use by ectotherms have traditionally been addressed in the context of thermal biology (e.g., Cowles and Bogert, 1944; Diaz, 1997; Huey, 1991; Huey et al., 1989; Humphreys, 1978; Porter and Tracy, 1983; Porter et al., 1973). However, the role of moisture in refuge choice by desert ectotherms has not, to our knowledge, been specifically investigated (but see Bulova, 2002). Vapor pressure deficit is presumably important because burrow micro-environments with lower vapor pressure deficits provide a reduced gradient for evaporative water loss, thereby facilitating conservation of body water. A fruitful area of future research would be to explore the consequences of spatial and temporal variation in moisture content of desert micro-environments, particularly refugia, for the ecology of desert ectotherms (see Tracy and Walsberg, 2002).

Shelter-site selection may also have important consequences for energy conservation. Gila Monsters spend the vast majority of their time relatively deep within shelters (>0.75 m), where body temperatures equilibrate to ambient temperature (D. Beck, 1990; personal observation). At our study site, *Heloderma suspectum* spent >50% of the year at body temperatures <20 C (unpublished data). Such

TABLE 3.—Seasonal variation in temperature and vapor pressure deficit (VPD in kPa) in 27 Gila Monster shelters monitored from January 1995 to August 1996. Values are means for all shelters combined \pm one standard error. Values with the same superscript did not differ significantly.

	Spring	Dry summer	Wet summer/fall	Winter
Temperature °C	19.8 \pm 0.21 ²	26.8 \pm 0.28 ³	27.2 \pm 0.26 ³	13.3 \pm 0.253 ¹
VPD	0.297 \pm 0.018 ¹	0.260 \pm 0.020 ²	0.210 \pm 0.017 ²	0.236 \pm 0.017 ²

behavior could be regarded as sub-optimal for vertebrate ectotherms, because foraging opportunities are lost when time is spent at reduced body temperatures while hiding from predators in shelters (Downes, 2001). Moreover, conserving heat while inside shelters may be important for lizards that are active on a daily basis (Christian et al., 1984; Huey et al., 1989). Helodermatid lizards, on the other hand, may actually benefit from lower body temperatures, and consequently reduced energy expenditure, during long periods spent inside shelters. This idea is somewhat supported by a previous finding that resting helodermatids have among the lowest metabolic rates of any lizard measured, with a metabolic Q_{10} of 3 between 25 C and 15 C (metabolic rate decreased three-fold with a 10 C drop in temperature) (Beck and Lowe, 1994). Hence, energy savings were greater at reduced temperatures. For Gila Monsters, the consequent reduction in metabolic rate may represent considerable energy savings particularly because frequent foraging activity on the surface is not necessary.

Other reptiles show voluntary hypothermia, or metabolic depression, even when environmental conditions provide thermal options for activity and precise thermoregulation (Christian et al., 1984; 1996a, 1999a; Dorcas and Peterson, 1998; Peterson, 1987; Regal, 1967; Zimmerman et al., 1994). The energetic advantages of voluntary hypothermia have been clearly demonstrated by several lizard species inhabiting seasonal tropical environments in Australia (Christian et al., 1996a, b, 1999a, b). Reduced body temperatures of individuals in shelters also translate into reduced rates of water loss (Mautz, 1980, 1982; Zimmerman et al., 1994). The choice of an appropriate refuge, therefore, is an important part of energy and water savings enjoyed by ectotherms that remain hidden below ground (Pough, 1980).

Seasonal Effects

We found that shelters selected by Gila Monsters during the hottest, driest time of year ("dry-summer" shelter type) were significantly less rocky, and remained significantly cooler and more humid throughout the year than those chosen in other seasons. Winter shelters, occupied for periods averaging nearly three months, were significantly rockier, warmer, and deeper than those used during other seasons. These results indicate Gila Monsters altered their choice of shelters as conditions changed seasonally. During the winter, when surface temperatures were frequently below freezing, Gila Monsters selected shelters with south-facing entrances on south-facing slopes that were rockier and deeper, and consequently warmer than shelters used in other seasons. During the dry summer, when surface temperatures were hot, and relative humidity very low, Gila Monsters selected shelters that were more variable in aspect, more soil-like in composition, and, consequently, cooler and moister than shelters used in other seasons. During the spring, when surface conditions were more benign and Gila Monsters were foraging, basking, searching for mates, and pairing within shelters, shelters were oriented more strongly toward the east, rockier, shallower, and, more variable in temperature and humidity than other shelter types.

Our results also suggest that the physical features of a shelter influenced its microenvironment. Shelter rockiness and depth significantly predicted shelter microenvironment, suggesting that physical characteristics influenced temperature and vapor pressure within Gila Monster shelters. Shallow, rocky shelters tended to be hotter and drier than deeper, soil-like shelters. Shelters with soil floors retained moisture better than rocky shelters and thus provided better refuge from the desiccating effects of low humidity

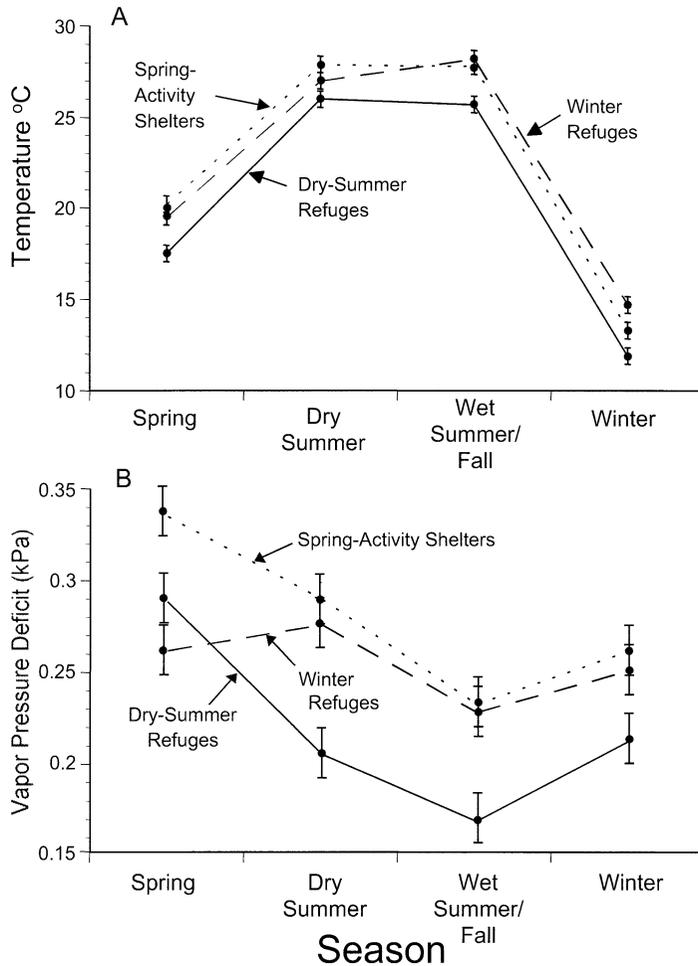


FIG. 5.—Seasonal variation in mean temperature (A) and vapor pressure deficit (B) among three shelter types monitored in this study. Horizontal bars designate \pm one standard error of the mean.

during the hot dry season. South-facing rocky shelters presumably captured more heat from the sun, especially during winter; entrances to east-facing shelters presumably warmed more quickly in the morning.

In other species of lizards and snakes rock size, especially thickness, affects the thermal properties of shelters which, in turn, influence refuge choice (Huey et al., 1989; Kearney, 2002). Velvet geckos select rocky-crevice shelters based on rock size, width, and height above ground (Schlesinger and Shine, 1994). Thermal properties are important cues in selection of refugia by other ectotherms as well (Burger and Gochfeld, 1991; Christian et al., 1984; Downes and Shine, 1998; Huey et al.,

1989; Humphreys, 1978). Rockiness may also be associated with shelter stability. At our study site, shelters found in soil and gravel substrata were susceptible to collapsing, and thus more ephemeral and less predictable as stable refugia.

Based on our results, aspect of shelter-site entrances may also be important to desert-dwelling organisms. Aspect undoubtedly influences thermoregulatory options at the shelter-site entrance. During the spring (March through May), Gila Monsters showed peak activity in the morning and often basked at shelter entrances prior to activity (Beck, 1990; this study). Their preference for east-facing shelters may therefore have allowed

TABLE 4.—Physical characteristics of Gila Monster shelters (rockiness, shelter depth) that possessed significant predictive power on shelter microenvironment (temperature and vapor pressure deficit) by season. Fall and wet summer shelters were combined in this analysis. Partial regression coefficients are shown in parentheses.

Season	Temperature	Vapor pressure deficit
Winter	Roof rockiness ($\beta = 52.41$) ($F_{1,45} = 7.28$, $P = 0.010$, $R^2 = 0.139$)	NS
Spring	NS	NS
Dry summer	Roof rockiness ($\beta = 96.45$)	Roof rockiness ($\beta = 116.26$)
	Shelter depth ($\beta = -64.38$) ($F_{2,38} = 5.58$, $P = 0.008$, $R^2 = 0.201$)	($F_{1,34} = 7.37$, $P = 0.010$, $R^2 = 0.151$)
Fall/wet summer	Roof rockiness ($\beta = 75.38$) ($F_{1,44} = 6.14$, $P = 0.017$, $R^2 = 0.101$)	NS

more efficient thermoregulation at shelter entrances at a time of year when basking behavior was more frequent.

Gila Monsters chose deeper shelters during seasons when surface conditions were most extreme (Winter and Dry Summer). Temperature and humidity stabilize beyond a certain depth within a shelter (Kay and Whitford, 1978; van Heerden and Dauth, 1987). Hence, deeper shelters likely provided a more stable microenvironment, allowing better refuge from harsh surface conditions (Kearney, 2002; Kinlaw, 1999). Desert Tortoises may also reduce water loss rates by choosing deeper burrows during hot, dry periods (Wilson et al., 2001).

There have been few investigations of seasonal variation in refuge use by desert ectotherms. Burrow use by Desert Tortoises (*Gopherus agassizii*) varies seasonally according to their social and thermal environments (Bulova, 1994; Zimmerman et al., 1994). In southern Australia, geckos respond to seasonal changes in thermal microenvironments by switching from retreats beneath rocks in spring to cooler, deeper crevices in summer (Kearney, 2002). Similarly, varanid lizards use shallower burrows in summer than in winter

TABLE 5.—Shelter fidelity and home ranges shown by 7 Gila Monsters outfitted with radiotransmitters between April and July 1992, and monitored at least weekly from November 1992 through June 1994 (Lizard no. 4's radio signal died in April of 1993).

Lizard no.	Sex	Total shelters	No. reused	Percent reused	Home range size (ha)
1	m	44	14	31.8	88.2
2	f	42	22	52.4	40.4
4	m	17	4	23.5	60.0
5	m	36	16	44.4	41.0
8	m	67	29	43.3	65.8
9	f	28	15	53.6	6.2
10	f	37	19	51.4	104.8
Mean				42.9	58.1

(King, 1980). These results, coupled with our findings, suggest that temporal variation in subsurface refugia are an important factor in habitat use by desert ectotherms and in their seasonal patterns of activity and dispersion.

Shelter Fidelity

Gila Monsters re-used nearly half of their shelters, but we suspect that is an underestimate of their actual shelter-site fidelity because the longer we tracked lizards, the more we observed them reusing previous shelter sites. In terms of time spent within shelters, Gila Monsters showed even greater fidelity to familiar sites, spending nearly eight times as long in reused shelters as in shelters observed to be used only once. Reused shelters tended to have rockier roofs than other shelters, a result probably attributable to their greater durability (shelters with soil roofs were vulnerable to collapse). Aside from rockiness, reused shelters were no different from shelters not observed to be reused. This result suggests that familiarity with a particular shelter may be an important cue in shelter-site selection. Sleepy Lizards (*Tiliqua rugosa*) use specific visual cues to recognize shelters and prefer familiar cues over novel ones; this may play a role in the fidelity they show to home range areas (Zuri and Bull, 2000). Cues other than structure or microenvironment may also be used; for example, shelter selection by Desert Tortoises is influenced by conspecific chemical cues (Bulova, 1997). Future work on shelter-site cuing in Gila Monsters would add an interesting dataset to be compared with the information on other organisms.

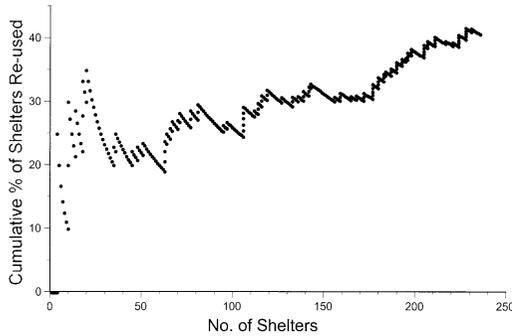


FIG. 6.—Approximately 43% of refugia were used more than once by Gila Monsters, a proportion that is clearly a function of duration of monitoring and sample size. This result, therefore, may be an underestimate of the actual proportion of shelters that are reused, and suggests that suitable refugia may be a limiting resource to Gila Monsters.

The patterns of shelter fidelity shown by Gila Monsters also suggest that different shelters serve different purposes, and these purposes varied seasonally. Many of the shelters reused during April through June were used by more than one individual, often two lizards at the same time. Males may fight during spring for access to particular shelters (Beck, 1990), and mating may take place in these shelters during April and June (Beck, 1990; Goldberg and Lowe, 1997; this study). Desert tortoises also show seasonal use of social shelters, where courtship and related reproductive behaviors may occur (Bulova, 1994). Therefore, these shelter sites apparently played a role in the social structure of the population.

In contrast to social shelters, other shelter-sites used by Gila Monsters during the dry summer appeared more important as refugia from harsh conditions on the surface. They were used by only one lizard, were deep and soil-like, and some were inhabited for periods up to 40 days. With one exception (a male-female pair), winter shelters were inhabited by only one lizard (interestingly, some individuals used overwintering shelters within a few meters of each other). Winter shelters had south-facing entrances, and were predictably rockier and deeper than shelters used in other seasons. Gila Monsters showed the greatest fidelity (73%) to these winter retreats, a result suggestive of the importance of reliable winter shelters that served as refugia from cold and

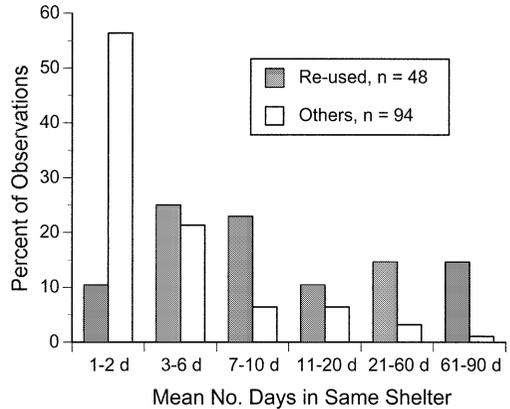


FIG. 7.—Plot of residence times in shelters. Gila Monsters spent nearly eight times as much time in reused shelters as in shelters used only once.

predators during >30% of the year (Beck, 1990; this study). Some lizards in our study returned to the same overwintering shelter for six consecutive winters.

Fidelity to shelter sites is not unique to Gila Monsters. Many other terrestrial vertebrate ectotherms, including snakes (Ciofi and Chelazzi, 1994; Reinert and Zappalorti, 1988; Webb and Shine 1997), lizards (Norris, 1953), tortoises (Bulova, 1994; Burge, 1977; Martin, 1995), and amphibians (Cohen and Alford, 1996) may show strong fidelity to specific retreats. Desert rodents are known to construct elaborate burrow systems that provide protection from predators and harsh surface conditions, and to which they show strong fidelity (Burns et al., 1989; Goyal and Ghosh, 1993; Murie and Michener, 1984;

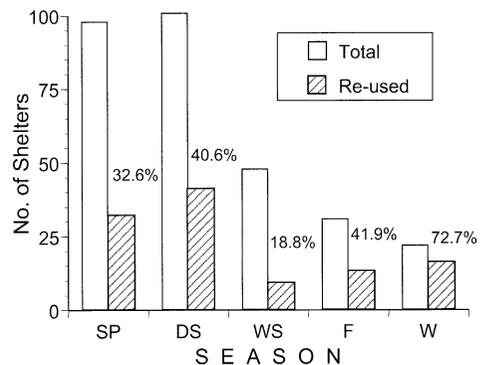


FIG. 8.—Shelter fidelity was significantly influenced by season. Gila Monsters showed the greatest fidelity to shelters used during extreme periods, such as winter.

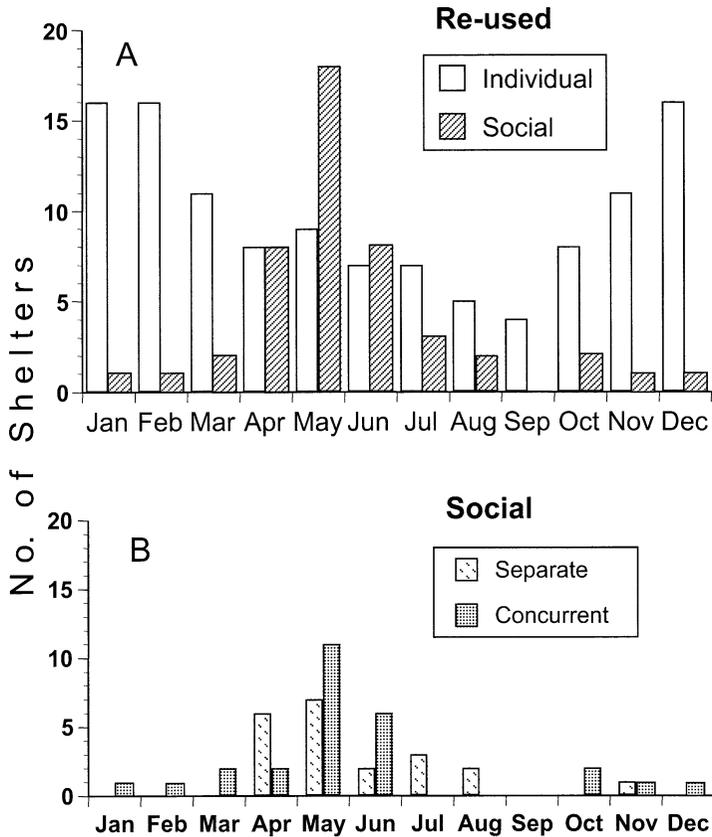


FIG. 9.—Seasonal variation in shelter use by Gila Monsters. (A) Individual shelters served as refugia from harsh surface conditions, such as winter cold and dry-summer heat. (B) “Social” shelters were used by more than one individual, sometimes concurrently. Gila Monsters inhabited shelters concurrently primarily during the spring when male-combat and mating occur.

Schmidt-Nielsen, 1964). Desert macroinvertebrates, including burrowing spiders (Humphreys, 1978; Marshall, 1997), scorpions (Polis et al., 1986), and beetles (Rasa, 1995) may also show fidelity to retreat-sites. Despite their differences, all these species share their dependence on suitable refugia, and their patterns of distribution and abundance may be related to the availability of suitable substrate in which burrows and shelter-sites can occur (Feldhamer, 1979; Kinlaw, 1999).

Conclusions

Our results illustrate how the ecology of a sedentary desert ectotherm is closely tied to its use of subsurface shelter sites. Shelters, and the habitats where they occur, were not chosen at random. Gila Monsters selected shelters based on specific structural and microenviron-

mental characteristics, altered their choice of shelters as conditions changed seasonally, and returned to preferred shelter sites year after year. Our results are also important because they suggest shelters may be a limiting resource for desert ectotherms, one that is often overlooked by ecologists interested in other factors affecting habitat use and patterns of activity, dispersion, and distribution. Selection of appropriate shelter sites is perhaps the most important means by which most ectotherms persist in extreme and variable desert environments. It is surprising, therefore, to find that this phenomenon has not been more extensively studied. Although physiological consequences of habitat selection for ectotherms have been recognized for some time (e.g., Huey, 1991), further research on the role of subsurface refugia in the ecology of desert

ectotherms might better explain their patterns of activity, behavior, distribution, and abundance.

Understanding the ecological importance and role of shelters in the natural history of organisms also carries implications for conservation. Conservation efforts aimed at identifying and protecting suitable habitats for sensitive species, for example, may need to make specific considerations of shelter sites as limiting resources. Knowledge of shelter characteristics, the abundance of shelters, and seasonal changes in shelter use may provide better tools for managing desert species threatened with habitat loss and human-related disturbance (Bulova, 1994; Zimmerman et al., 1994).

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