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ORIGINAL RESEARCH

Livin' la vida local: philopatry results in consistent patterns of annual space use in a long-lived lizard

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Abstract

For animals exhibiting range residency, the home range is a useful framework to quantify space use. Some reptiles can live decades in the wild and experience extreme environmental variation that influences patterns of habitat use. Individuals may modify their use of space over time, reducing the utility of single-year home range estimates. Very high frequency (VHF) telemetry data were collected for Gila monsters (*Heloderma suspectum*) at three Mojave Desert sites in Clark County, Nevada, and home range utilization distributions were calculated using an autocorrelated kernel density estimator. Home range size was consistent within individuals and populations, and home range size did not vary across years at any site. To measure home range fidelity (year-to-year reuse), we calculated Bhattacharyya's coefficient (BC) for each combination of years in which an individual was tracked and averaged estimates across individuals and populations. The average BC score was 0.86 (scale from 0 to 1; 0 = no overlap and 1 = complete overlap) and did not vary among populations. We modeled home range area accumulation to estimate the minimum sample size needed for asymptotic stability and found home range accumulation to be dynamic and variable within and across years and individuals. Analysis of the frequency of movement by individuals, average distance traveled per movement, and cumulative distance traveled per active season revealed that movement patterns vary considerably by year. Heterogeneity of space use among populations and individuals suggests that individual and local environmental variation, rather than annual variation in resource availability, may drive home range size and movement patterns of Gila monsters in southern Nevada. Annual variability in movement patterns did not translate to variability in home range size or location, and the species exhibits extremely high philopatry, using the same areas for periods of at least 3–5 years.

Introduction

Analysis of a species' spatial ecology can reveal important aspects of its biology, including resource selection, reproductive timing, thermal physiology, and territoriality, each of which can inform management and conservation decisions. A common and useful framework for understanding animal space use is the home range concept. It was first described as the area used by individuals in their regular activities of food gathering, mating, and caring for the young (Burt, 1943). This definition, though general and vague, reflects the nature of space use estimation as an analytical process specific to the biological system to which it is being applied and the method with which it is being estimated (Powell, 2000). There is increasing awareness of the importance of temporal scale (annual, seasonal, etc.) when attempting to draw biological inferences from home range estimates (Börger, Franconi, Ferretti, et al., 2006). Contemporary definitions of home range consider the estimate to be a prediction of an individual's future space use as a function of previously observed locations and movements (Fleming et al., 2015). An accurate home range estimate requires data collection at a temporal scale that captures the processes underlying movement decisions (Harris et al., 1990). Space use and movement may be shaped by extrinsic factors such as the distribution, seasonal availability, and quality of resources (Gerber et al., 2012; Haskell et al., 2002; Roe &

Georges, 2008), or by intrinsic factors such as sex, life stage, body size, and foraging mode (Averill-Murray et al., 2020; Christian & Waldschmidt, 1984; Garrison et al., 2017; Perry & Garland, 2002; Verwaijen & Damme, 2008). Thus, space use changes as a function of both predictable (i.e., seasonal, Ariano-Sánchez et al., 2020; Brito, 2003) and unpredictable factors (i.e., stochastic environmental variation, Rivrud et al., 2010; Van Beest et al., 2011). Because animals can respond to changes in environmental suitability by modifying space use and movement, it is important to monitor individuals over sufficient durations to document these responses at a species level (Clutton-Brock & Sheldon, 2010). Studies that include few individuals or short tracking durations may yield a biased perspective that is primarily driven by short-term variation in environmental conditions or individual variation and may not reflect typical space use by the species (Schneider, 2001).

Substantial effort has been put forth in developing space use estimators that, with sufficient sampling, produce stable home range estimates that do not change markedly when additional relocations are added (Börger et al., 2008; Van Moorter et al., 2009). In theory, a home range size estimate that reaches an asymptote with increased sampling would represent an animal's lifetime space use. Regardless of their shape, home range accumulation curves may provide temporal and biological context to home range estimates. Decreases in space use may reflect an individual's encounter with a productive resource patch or a seasonal shift under a less favorable environment where movement becomes costly as resources diminish (Gerber et al., 2012; Hawkes et al., 2011). Increases in space use may reflect mate-searching behavior or a scarcity of resources in preferred areas or habitat patches (Brito, 2003; Rivrud et al., 2010). Asymptotic home range estimates have been reported for minimum convex polygon (MCP; Hinderaker, 2021; Wolfe & Hayden, 1996) and kernel density estimation methods (KDE; Plotz et al., 2016), although other studies found that some home range estimates never reached an asymptote (Gautestad & Mysterud, 1995; Medri & Mourão, 2005). This inconsistency suggests that home range asymptotes may not exist for all species or study areas. Home range estimates which accumulate asymptotically have been used to infer a minimum necessary sampling duration and temporal sampling regime for future studies (Bekoff & Mech, 1984; Börger, Franconi, De Michele, et al., 2006; Seaman et al., 1999).

Species with long life spans tend to experience greater temporal variation of resource availability and thus are likely to use space in a way that is most appropriately described through both short (e.g., annual) and long (e.g., multi-year) investigations. The inclusion of varied temporal scales provides a meaningful context for lifetime space use. The Gila monster (*Heloderma suspectum*) is long-lived and inhabits highly variable resource environments. They are large-bodied and secretive lizards that can live more than 20 years (Bowler, 1977; Crosman, 1956; Jennings, 1984; Snider & Bowler, 1992). They occur in desert and thorn scrub habitats throughout the southwestern United States and northwestern Mexico, and although generally dry and warm year-round, these habitats are characterized by high climatic variability, especially in seasonal and annual temperature and precipitation (Sheppard et al., 2002). Their longevity increases the likelihood of experiencing environmental variation (in temperature, precipitation, food availability, etc.) and thus provides a natural context for examining temporal variation in space use.

Gila monsters possess several physiological and behavioral adaptations for surviving periods of resource scarcity that result from environmental variation. They have an exceptionally low metabolic rate which, when paired with extreme inactivity, allows them to endure extended periods of resource scarcity (Beck & Lowe, 1994; Gienger et al., 2014). Beck (2005) estimated that a Gila monster can meet its minimum metabolic requirement with only three meals per year, and when more food is available, they can consume large quantities and store fat in their tails (Beck, 1990; Bogert & Martín del Campo, 1956; Stahnke, 1950). They also use their bladder as a water reservoir to buffer dehydration during periods of drought (Davis & DeNardo, 2007). The ability to store fat and water affords individuals the ability to remain quiescent underground in times of low food and water availability (Hughes et al., 2021). The species' physiological adaptations to resource scarcity and fluctuation suggest that they are significant constraints. Gila monsters may also use behavioral mechanisms for coping with such constraints (e.g., modifying space use in response to resource availability) and so we expected observed variation in space use (regardless of magnitude) to correspond to annual cycles of environmental change. Gila monsters exhibit high fidelity to underground shelters that they use for thermal refuge and mating (Beck & Jennings, 2003; Brown, 2021) and have strong philopatry to core areas within their home range (Beck, 2005; Pierson, 2020). These core areas may contain relatively predictable resources (food, shelter, mates, etc.) which shape and constrain their movement patterns to produce relative consistency in spatial habitat use across years.

We tested the hypothesis that patterns of spatial habitat use in Gila monsters are shaped jointly by the species' notable longevity, routine exposure to environmental variation, and philopatry to suitable habitat areas. We expected relative consistency in spatial habitat use across years, with observed variation in space use (regardless of magnitude) corresponding to annual cycles of environmental change.

Materials and methods

Study sites

Data were collected at three locations in Clark County, Nevada (referred to as sites A, B, and C to protect exact population locations). Sites were within the Mojave Desert, which typically receives less than 25 cm of rain annually (Hereford et al., 2006). Elevation at the field sites was 400–900, 600–1500, and 1000–1500 m for sites A, B, and C, respectively, and the dominant vegetation community was Mojave desert scrub (Turner, 1994). Site A was the same site studied by Gienger (2003) from 2001 to 2002, but we collected data over an additional two years as well (2003–2004). This site was

sparsely vegetated relative to the others, primarily by creosote (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and brittlebush (*Encelia farinosa*), with some portions intersected by roads. Site B was especially rocky with creosote, cacti (*Opuntia* sp., *Cylindropuntia* sp.), and Mojave yucca (*Yucca schidigera*) and no buildings or paved roads. Site C bordered a small residential area and had a spring system that supplied water most of the year, promoting continual and diverse vegetation growth, including riparian species such as cottonwoods (*Populus* sp.) and ash (*Fraxinus* sp.). Common species included creosote, blackbrush (*Coleogyne ramosissima*), white bursage, Anderson thornbush (*Lycium andersonii*), and hedgehog cacti (*Echinocereus engelmannii*). All sites were protected natural areas.

Data collection

Gila monsters were found using visual encounter surveys conducted on foot. We placed emphasis on areas with the best habitat, tracks, or reports/sightings from the public. Once located, Gila monsters were captured and surgically implanted with a 15 g very high frequency (VHF) radio transmitter into the coelomic body cavity (Holohil Systems, Ottawa, ON, Canada or Telonics, Mesa, AZ, USA). Lizards were kept overnight following surgery and were generally released 24–48 h after the procedure at the site of capture. Telemetry antennas (Telonics) and receivers (Advanced Telemetry Systems, Isanti, MN, USA) were used to home in on the study individuals and locations were recorded using a handheld GPS unit (Garmin, Olathe, KS, USA) and/or ArcGIS Survey123 (Esri, Redlands, CA, USA). Most data (62%) were collected between April and August, during the Gila monster's activity and breeding seasons (Beck, 2005). Lizards were relocated as frequently as possible given available manpower for each study site; once every 1.0 ± 2.5, 5.6 ± 5.9, and 3.3 ± 4.8 days at sites A, B, and C, respectively. Study durations were 1161 days (2001–2004), 1499 days (2013–2017), and 2030 days (2016–2021), respectively. See Tables S1 and S2 for more information regarding sample sizes and sampling regimes.

Data analysis

Analyses were performed using R (v4.2) for statistical computing (R Core Team, 2021) within RStudio (v2022.7.2, RStudio Team, 2022). Where linear models were used, model assumptions were evaluated using *check_model* function in the R package *performance* (v0.10, Lüdecke et al., 2021). All active season relocation points (observations made after Spring emergence from brumation until entering brumation the following Fall) were used for spatial analyses along with one overwintering point (the individual hibernaculum) because repeated relocations of lizards in overwintering shelters would downweight active season locations and negatively bias estimates (Fleming & Calabrese, 2017). We calculated utilization distributions on both cumulative and annual scales for datasets with at least 30 observations using optimally weighted area-corrected autocorrelated kernel density estimation (wAKDE$_c$) via the package *ctmm* (v1.0, Calabrese et al., 2016). AKDE estimates are

robust to the temporal autocorrelation present in nearly all animal tracking data and to which reptiles are particularly prone (Bruton et al., 2014; Crane et al., 2021; Fleming et al., 2019; Guarino, 2002; Hailey, 1989; Noonan et al., 2019). wAKDE accounts for irregular sampling regimes by upweighting observations during under-sampled periods and downweighting observations during over-sampled periods (Fleming et al., 2018), and AKDE$_c$ accounts for small sample sizes (Fleming & Calabrese, 2017). Thus, wAKDE$_c$ (herein referred to as AKDE unless otherwise noted) is a nonparametric improvement upon existing kernel density estimators.

To evaluate home range area accumulation for individuals over time, a cumulative AKDE estimate was calculated for data subsets starting with 30 observations and increasing at an interval of five consecutive observations until all relocations for an individual were used. Unweighted AKDE was used for accumulation calculations as it required significantly less computation time (days vs. weeks). Home range area accumulations were plotted against sample size and the shapes of the accumulation curves were visually examined. Individuals were assigned to one of four accumulation types: increasing, decreasing, stable, and stochastic. Increasing and decreasing accumulation types were characterized by a home range that consistently increases or decreases or does so to an asymptote. Stable accumulation was characterized by a relative lack of change in home range size, and stochastic accumulation appears to be random or a combination of other accumulation types.

To quantify annual home range overlap for individuals tracked for multiple years and test our prediction that home range will remain relatively stable, bias-corrected Bhattacharyya's Coefficients (BCs) were calculated using the *overlap* function from *ctmm*. The BC is approximately the ratio of the area of the intersection of two distributions to the average area of the individual distributions and is easier to interpret and compare than directional methods that provide two estimates per pair of home ranges (Winner et al., 2018). To address change in home range shape over time, BC was calculated for every combination of years (consecutive and non-consecutive) an annual home range estimate was calculated. Because individuals were not sampled evenly (i.e., tracked for the same number of years), marginal means of overlap were calculated using the *emmeans* function and package (v1.7, Lenth, 2022) to address disproportionate contributions of over- and under-sampled individuals.

Annual movement metrics were calculated for every individual that was tracked for more than 90 days within a year to ensure that data spanned most of an active season. A lizard was considered to have moved if the straight-line distance between two consecutive relocation points was more than 20 m. Although Gila monsters are known to occasionally move shorter distances, such movements were indistinguishable from GPS or observer error (because the animals are usually underground, the exact location can be difficult to detect) and were excluded. A total number of movements, frequency of movement, average movement distance, and cumulative movement distances were calculated for each individual in each year. Marginal means (to account for an uneven sampling of

individuals) of the latter three metrics were calculated with *emmeans* using models in which the response variable was the movement metric and animal ID was a fixed effect.

Differences in AKDE home range size estimates among populations were evaluated using linear models. For the cumulative analyses (one estimate per lizard), we used the Model 1 formula (Table 1). For annual analyses (each lizard having estimates across multiple years), a linear mixed-effects model was used (Model 2, Table 1). All mixed-effect models were built using *lme4* (v1.1, Bates et al., 2015). Animal ID was considered a random effect to account for repeated sampling of individuals across multiple years. Tukey's pairwise comparisons were evaluated using the *emmeans* package. To estimate the influence of population on home range overlap, a linear mixed-effects model was used (Model 3, Table 1). Differences in annual home range size estimates among individuals were evaluated using a linear model (Model 4, Table 1). For estimates of the influence of year on home range size and movement metrics (total number of movements, frequency of movement, average movement distance, and cumulative movement distance), populations were analyzed separately because there was minimal overlap in years that lizards were tracked across populations (Model 5, Table 1). We estimated the influence of home range size on interannual overlap using Model 6 (Table 1).

The repeatability (the proportion of variation that can be attributed to between-group variation, Nakagawa & Schielzeth, 2010) of annual home range size and movement metrics (frequency of movement, average distance per movement, and cumulative distance moved per active season) across years was assessed using the package *rptR* (v0.9, Stoffel et al., 2017). For repeatability of home range size, see Model 7 (Table 1), and for repeatability of movement metrics, see Model 8 (Table 1). Linear mixed-effect models were used to compare movement metrics across populations (Model 9, Table 1). A chi-squared test was used to assess whether observed frequencies of each home range area accumulation type (increasing, decreasing, stable, or stochastic) differed from expected.

Table 1 Formulas of the models used to analyze spatial data of Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021

Model	Formula
Model 1	hr ~ pop + n
Model 2	hr ~ pop + n + (1|id)
Model 3	overlap ~ pop + (1|id)
Model 4	hr ~ id + n
Model 5	metric/hr ~ year + (1|id)
Model 6	marginal mean overlap ~ cumulative hr
Model 7	hr ~ n + (1|year) + (1|id) + (1|pop)
Model 8	metric ~ n + d + (1|year) + (1|id) + (1|pop)
Model 9	metric ~ pop + (1|id)

Home range is abbreviated as hr, population as pop, sample size as n, animal ID as id, and movement metric as metric.

Results

Home range

Forty-one individuals were tracked during the study (12, 10, and 19 from sites A, B, and C, respectively). Across all sites, individuals were relocated 226 ± 215 (mean ± SD) times (the number of relocations ranged from 40 to 767). Individuals were relocated an average of 457 ± 241, 77 ± 47, and 159 ± 115 times at sites A, B, and C. A total of 24 individuals had sufficient sample sizes and sample durations to be used in multi-year analyses (10, 3, and 11 from each site respectively). Mean cumulative home range area (estimate including all observations in all years) was 112 ± 99 ha and the marginal mean annual home range area for individuals was 111 ± 114 ha. Home range size varied by population for both cumulative ($F_2 = 7.71$, $P = 0.002$) and annual ($F_{2,56} = 7.00$, $P = 0.002$) estimates (Table 2), with lizards at site A having larger annual and cumulative home ranges than those at site C, and lizards at site A having larger annual home ranges than those at site B (Table 3). Annual home range size also varied by individual ($F_{34} = 2.96$, $P = 2.05 \times 10^{-4}$).

Repeatability of annual home range sizes was high within individuals ($R = 0.288$, $P = 3.95 \times 10^{-5}$) and populations ($R = 0.286$, $P = 0.031$; Fig. 1) but was much lower within each year ($R = 0.042$, $P = 0.127$; Fig. 2), which contrasted our prediction that year would be a significant contributor to variation in home range size. Annual home range size did not vary among years for any population (A, $F_{3,26} = 2.97$, $P = 0.050$; B, $F_{3,7} = 0.96$, $P = 0.463$; C, $F_{5,26} = 1.12$, $P = 0.376$). Marginal mean home range overlap (Bhattacharyya's Coefficient) was 0.86 ± 0.079 among individuals and did not differ statistically among populations ($F_{2,17} = 1.075$, $P = 0.363$; Fig. 3), supporting our prediction that Gila monsters would exhibit relative consistency in space use.

We had sufficient sample sizes to calculate home range accumulation for 35 individuals. Home range accumulation type varied across individuals, with accumulation curves falling into one of four categories (Fig. 4): stable (8/35 individuals; 23%), increasing (4/35 Individuals; 11%), decreasing (13/35 Individuals; 37%), or stochastic (10/35 Individuals; 29%). Observed values do not differ from the expected value of 8.75 individuals for each category, $X^2(3, N = 35) = 4.886, P = 0.180$.

Table 2 Mean (cumulative) or marginal mean (annual), standard deviation (SD), and range (minimum-maximum) of optimally weighted area-corrected autocorrelated kernel density estimator (AKDE) home range size by population of Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021

	Annual home range (ha)			Cumulative home range (ha)		
Population	Mean	SD	Range	Mean	SD	Range
A	180.3	142.0	27.7–535.1	184.4	128.4	27.8–452.7
B	96.7	61.8	26.3–198	121.5	70.4	38.7–247.7
C	66.3	81.4	8.6–356	60.6	53.2	10–237.5

Annual home ranges were calculated for each individual in each year it was tracked. Cumulative home ranges were calculated for each individual using all relocations across all years it was tracked.

Table 3 Post-hoc pairwise comparisons of mean home range size across populations of Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021

Contrast	Annual home range			Cumulative home range		
	df	*t* Ratio	*P* value	*df*	*t* Ratio	*P* value
A – B	41.8	2.59	0.034	37	1.73	0.208
A – C	38.5	3.60	0.003	37	3.43	0.004
B – C	34.7	0.05	0.999	37	1.62	0.251

Home ranges were calculated using optimally weighted area-corrected autocorrelated kernel density estimation (AKDE). Annual home ranges were calculated for each individual in each year it was tracked. Cumulative home ranges were calculated for each individual using all relocations across all years it was tracked.

Movement

During the active season (emergence through ingress for brumation), 34 lizards for which we had sufficient data for analyses moved an average of 32.16 ± 10.59 times (1.13 ± 0.38 movements week^{-1}). Between relocations, individuals traveled an average of 248.83 ± 74.98 m. Frequency of movement (mean = 1.13 ± 0.38 movements week^{-1}, $F_{2,85} = 2.024$, $P = 0.139$) and cumulative distance traveled per active season (mean = 15906.27 ± 6900.49 m, $F_{2,85} = 2.57$, $P = 0.093$) did not vary across populations, but average distance per movement did (mean = 248.83 ± 74.98 m, $F_{2,30} = 4.40$, $P = 0.021$). Lizards at site A traveled farther per movement than those at site C, but lizards at site B did not differ from lizards at either of the other sites (Table 4, Fig. 5).

Frequency of movement was repeatable within individuals ($R = 0.120$, $P = 0.044$) and years ($R = 0.522$, $P = 3.03 \times 10^{-9}$) but not populations ($R = 0$, $P = 1$). Average distance traveled per movement was repeatable within individuals ($R = 0.270$, $P = 5.21 \times 10^{-6}$), populations ($R = 0.327$, $P = 0.027$), and within each year ($R = 0.161$, $P = 0.002$). Cumulative distance traveled per active season was repeatable within individuals ($R = 0.234$, $P = 3.49 \times 10^{-4}$) and within each year ($R = 0.459$, $P = 5.10 \times 10^{-9}$) but not within populations ($R = 0$, $P = 0.500$).

Within populations, year influenced movement rate (A: $F_{3,17} = 27.14$, $P = 9.43 \times 10^{-7}$, B: $F_{3,3} = 7.00$, $P = 0.077$, C: $F_{5,24} = 7.63$, $P = 2.11 \times 10^{-4}$), average distance traveled per movement (A: $F_{3,18} = 10.51$, $P = 3.48 \times 10^{-4}$, B: $F_{3,5} = 0.69$, $P = 0.597$, C: $F_{5,20} = 5.11$, $P = 0.004$), and cumulative distance traveled per active season (A: $F_{3,17} = 37.63$, $P = 1.08 \times 10^{-7}$, B: $F_{3,5} = 1.44$, $P = 0.337$, C: $F_{5,21} = 5.91$, $P = 0.001$) at sites A and C but not B.

Discussion

Long-term tracking data from three populations of Gila monsters enabled the examination of spatial ecology at a time scale (up to 6 years) that is relevant given the species' longevity (likely more than 20 years in the wild). Despite inhabiting environments characterized by pronounced variations in temperature and precipitation, Gila monsters exhibit patterns of space use that are relatively stable across years. Annual AKDE home range size is repeatable across years, and year-to-year overlap of annual home ranges within individuals is high. This is consistent with the "always-stay" settlement strategy thought to be optimal in unpredictable environments because when the outcome (reproductive success, fat storage, etc.) of previous years is not predictive of the quality of resources within a patch in upcoming years, resettlement is unlikely to yield benefits that outweigh its risks (Byer & Reid, 2022; Switzer, 1993).
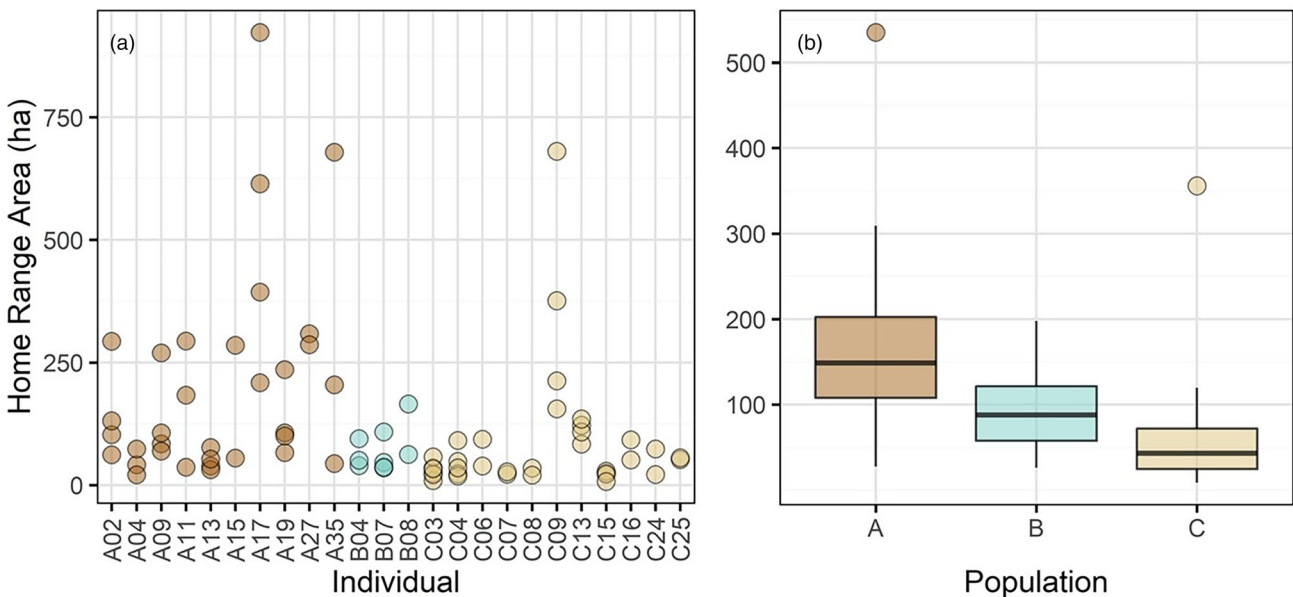

Figure 1 Annual home range size of Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021 by individual (a) and population (b). Home range size was calculated using optimally weighted area-corrected autocorrelated kernel density estimation (AKDE). Boxplots (b) show the distribution of marginal means for each individual measured across multiple years (a).
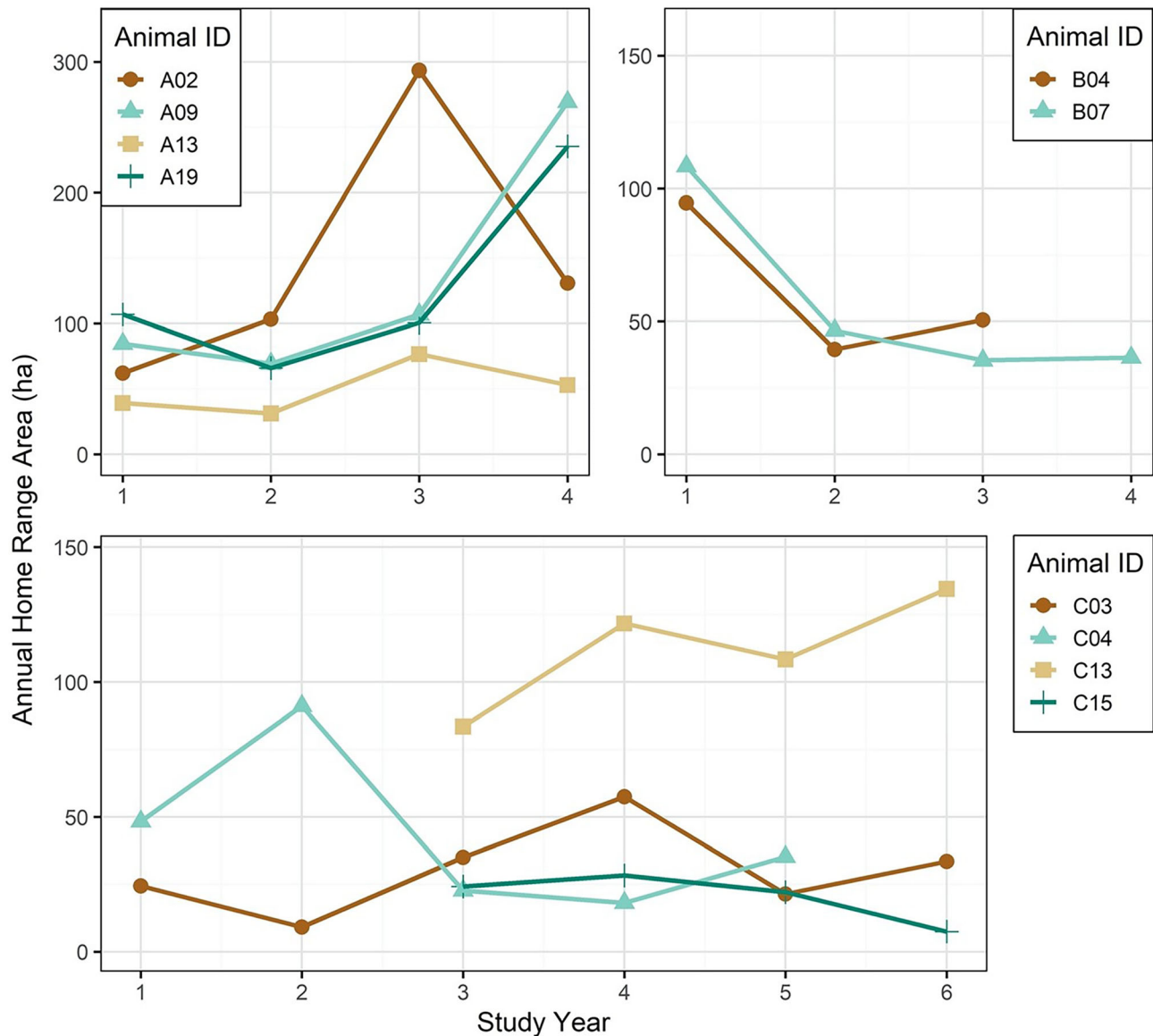
Figure 2 Variability in annual home range size over time of the longest-tracked individuals from three populations of Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021. Home range size was calculated with optimally weighted area-corrected autocorrelated kernel density estimation (AKDE).

Cumulative and marginal mean annual AKDE home ranges were comparable in size. Compared to annual home ranges, cumulative home ranges generally fell within the middle of the distribution for individuals tracked across multiple years. Cumulative home ranges seem to be a good representation of overall space use that is not skewed by the variability of individual years (Fig. 6), whereas annual home ranges provide a snapshot of space use that may provide a more nuanced view of home range variability (Fig. 4).

The sizes of both annual and cumulative home ranges varied among and within populations. Lizards tended to have similar space use each year they were tracked, but there was considerable variability among individuals both within and across sites.

Habitat and resource availability may drive space use, with individuals who occupy less productive areas potentially foraging more widely each year to meet their energetic needs. Previous studies found that tortoises (Testudinidae) respond to variation in resource availability across habitat types and seasons by modifying their home range size, movement patterns, and displacement distances (Castellón et al., 2018; Geffen & Mendelssohn, 1988; McMaster & Downs, 2009). A similar effect of seasonality has been noted in Guatemalan beaded lizards (*Heloderma charlesbogerti*), which have smaller home ranges, smaller core areas, and shorter movements during the dry season (Ariano-Sánchez et al., 2020). In Gila monsters, individuals can dramatically alter space use in response to food
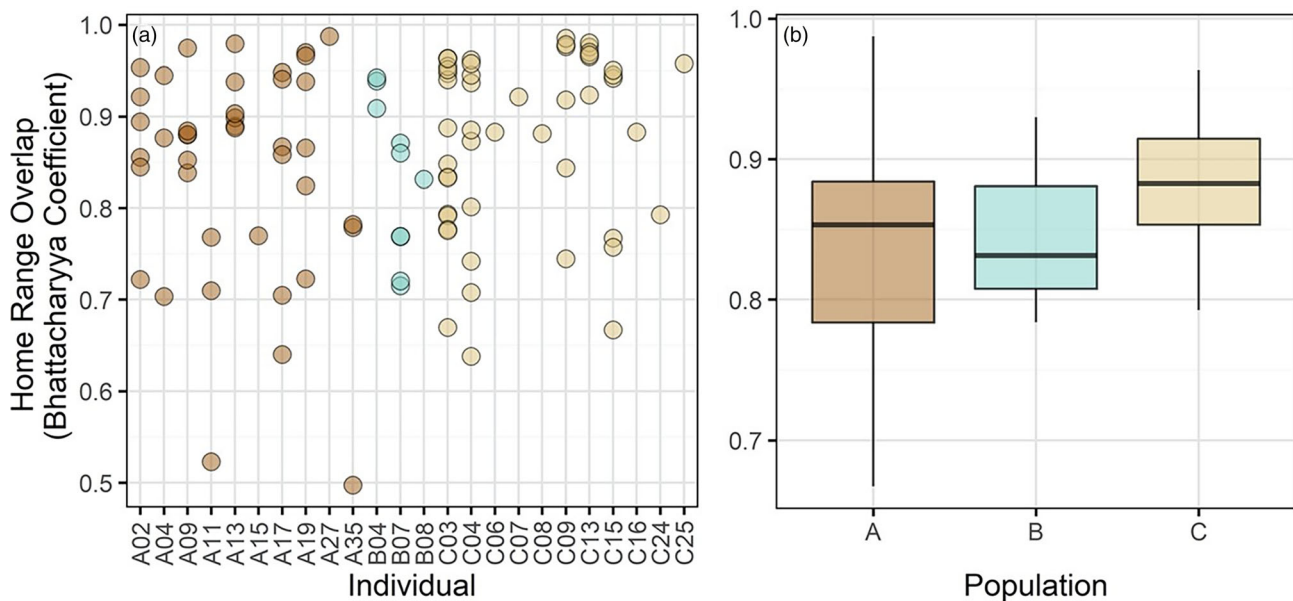
Figure 3 Overlap of annual home ranges (95% utilization distributions) of Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021 by individual (a) and population (b). Home ranges were calculated with optimally weighted area-corrected autocorrelated kernel density estimation (AKDE). Each circle (a) represents the overlap of 2 years; all possible combinations of years for each individual were used. Boxplots (b) show the population distribution of marginal mean overlap for individuals measured across multiple years (a).

and water subsidies (Pierson, 2020), demonstrating the importance of resource availability to their spatial ecology. In subsidized environments, individuals had up to 66% smaller home ranges than individuals at natural sites. Additionally, males overlapped less with male neighbors and females overlapped more with female neighbors at the subsidized site. Male Gila monsters tend to have larger home ranges than females due to mate-searching behavior during the breeding season (Gallardo, 2003; Kwiatkowski et al., 2008; Pierson, 2020). Thus, intrinsic factors such as sex and age are also likely important drivers of the inter-individual variation in home range size (Payne et al., 2022; Schoener & Schoener, 1982) and may have an additive or interactive effect with small-scale habitat quality/characteristics.

Individuals had a similarly sized home range each year they were tracked. Differences in space use across years may be explained by variations in individual characteristics that shape behavior (e.g., sex, age, or individual idiosyncrasies) or patterns that occur at scales other than annually (e.g., seasonally, Gallardo, 2003; Pierson, 2020). Alternatively, lizards may adapt their annual space use in ways that are not reflected in a size estimate. For example, if individuals modify the intensity with which they use resources within their home range, they could meet their needs without changing the boundaries or size of their home range. Payne et al. (2022) observed such shifts in areas of highest use in sleepy lizards (*Tiliqua rugosa*), which, like Gila monsters, are long-lived lizards with high philopatry (Bull & Freake, 1999). Some sleepy lizards used the same home range area across study years but modified the intensity with which they used different patches within the home range. Lower body mass, larger increase in mass

between years, fewer interactions with neighbors, higher conspecific overlap, and longer time between measured years were all associated with decreases in fidelity to home range cores (Payne et al., 2022). Other lizards, such as Cunningham's skinks (*Egernia cunninghami*), exhibit high philopatry to the place they are born and rarely travel outside of a small area (Stow & Sunnucks, 2004). Results from Gila monsters in our study provide evidence that year-to-year fluctuations in individual home range size are small in magnitude over the course of 3–5 years, which is comparable to sleepy lizards (Bull & Freake, 1999) and Cunningham's skinks (Stow & Sunnucks, 2004).

Philopatry is an important aspect of spatial ecology in many species and several studies have demonstrated the value of familiar spaces in influencing fitness-related activities, including predator avoidance, territory acquisition, and foraging (Stamps, 1987, 1995; Stephens & Krebs, 1986). The willingness of the Gila monster to endure thermal, energetic, and predation risk to return to the site of origin after translocation (Sullivan et al., 2004) emphasizes the importance of home range site fidelity. Gila monsters have a low preferred body temperature and thermal tolerance relative to other lizards (Bogert & Martín del Campo, 1956; Brattstrom, 1965; Gienger et al., 2013) despite inhabiting hot environments. They rely primarily on behavioral thermoregulation and staying within familiar habitat areas allows Gila monsters predictable access to known refuges (Gienger, 2009). High-quality thermal refugia are in limited quantity throughout the landscape (Beck & Jennings, 2003), prompting Gila monsters to reuse the same shelters, sometimes for decades (Brown, 2021; Gienger et al., 2021). Staying in a familiar area with close proximity to
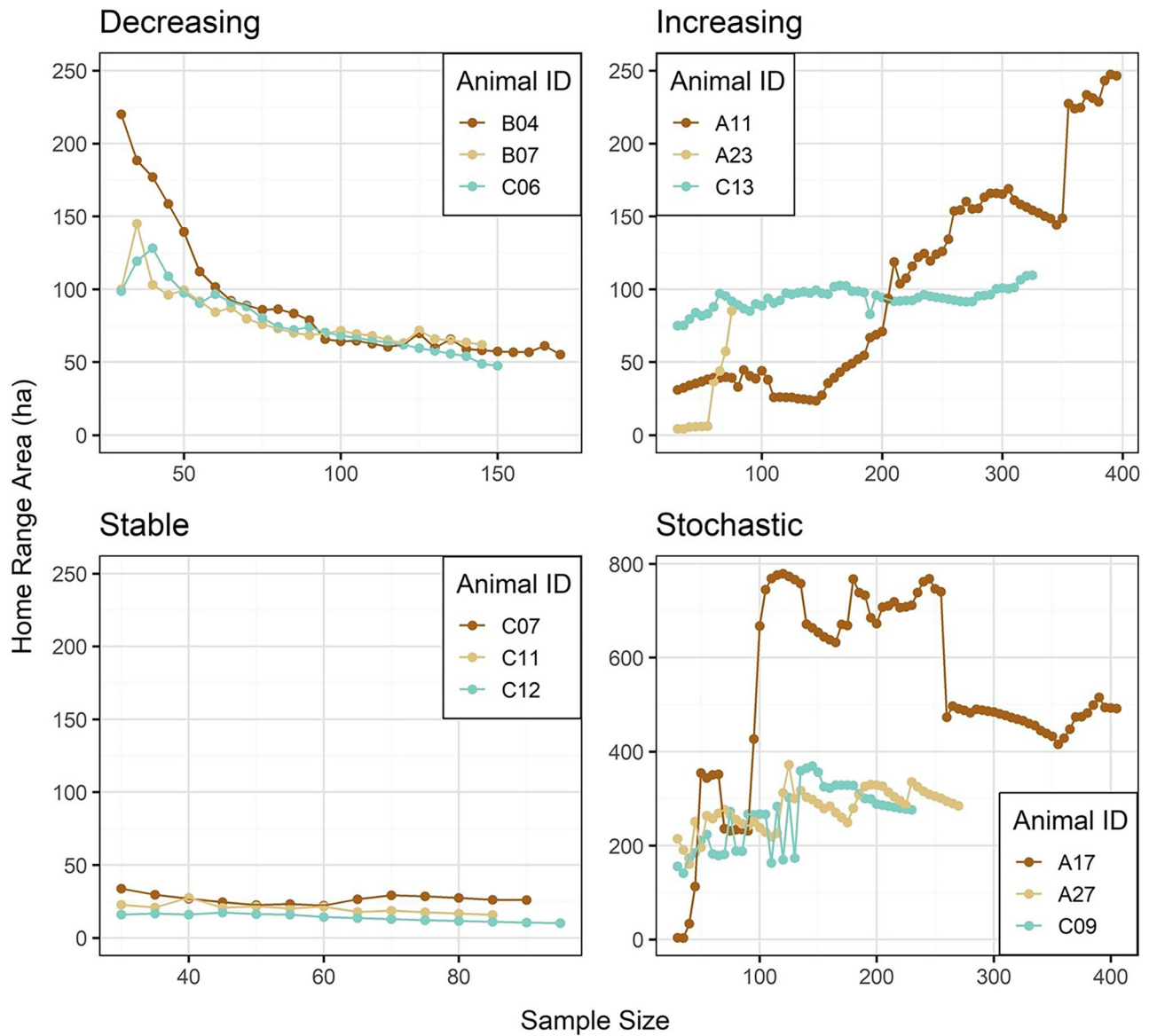
Figure 4 Example patterns of home range area accumulation as a function of sample size (number of relocations) for Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021. Estimates are cumulative across years with all observations considered consecutively. Home ranges were calculated with area-corrected autocorrelated kernel density estimation (AKDE).

Table 4 Post-hoc pairwise comparisons of marginal means for three movement metrics among populations of Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021

Contrast	No. of movements			Distance per movement			Cumulative distance		
	df	*t* Ratio	*P* value	*df*	*t* ratio	*P* value	*df*	*t* Ratio	*P* value
A − B	30.6	1.74	0.205	32.3	0.62	0.811	30.7	1.77	0.196
A − C	21.9	−0.23	0.972	27.8	2.89	0.020	22.5	1.92	0.156
B − C	30.8	−1.93	0.148	34.3	1.51	0.298	31.2	−0.44	0.898

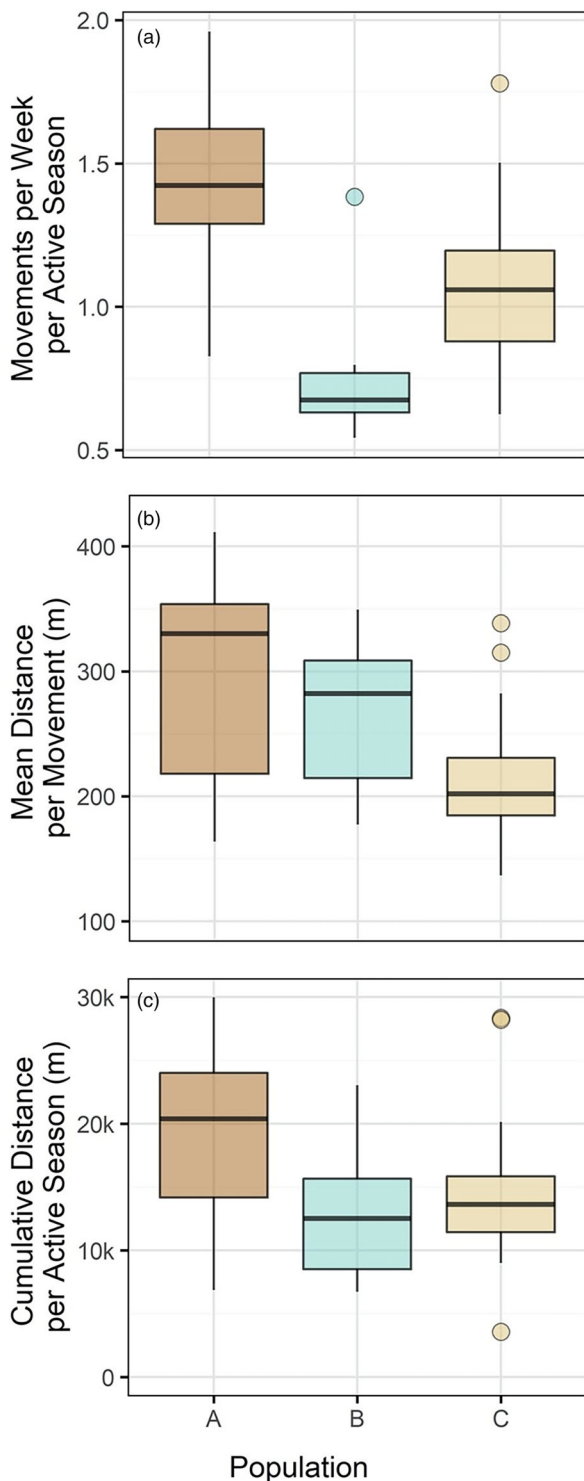Metrics were calculated for each individual in each year it was tracked.

Figure 5 Frequency of movement, average distance per movement, and cumulative distance per active season by population of Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021. Metrics were calculated for each individual in each year it was tracked.

known shelters may be a strategy to reduce thermal risk and economize energy expenditure. Surface activity for foraging and mate acquisition is a proportionally large part of the annual energy budget (Gienger et al., 2014), so minimizing exploratory movements has potential energetic benefits, particularly in periods of low prey availability.

Individuals in this study exhibited at least four types of AKDE home range accumulation. There was notable heterogeneity of shape within and across accumulation curve types (increasing, decreasing, stable, and stochastic; Fig. 4), and individuals varied in the timing and magnitude of change in home range size. Other studies have found similar variability in home range accumulation (de Almeida Jácomo et al., 2013), even with asymptotic accumulation (Harris et al., 1990), though failure to reach an asymptote is not uncommon (Carter et al., 2012; Cobarrubia-Russo et al., 2020; Emmons et al., 2012). Although diverse patterns of home range accumulation are well documented, the patterns observed in this study were particularly varied. Many individuals did not exhibit clear home range asymptotes despite large sample sizes and confirmed range residency. This lack of asymptotic home range accumulation may be due to the unique movement patterns of Gila monsters; they exhibit sporadic long-distance movements followed by long durations of inactivity (Beck, 1990). Area accumulation curves are useful for identifying temporal patterns and deviations from normal space use such as dispersal, range shifts, or transient behavior (Harris et al., 1990). For many species and/or populations, home range size is a snapshot of space use which can potentially lead to the misinterpretation that it is static and stable. The diversity within the area accumulation curves demonstrates the dynamic nature of space use, even among highly philopatric species.

During bouts of movement, individuals traveled about the same distance as Gila monsters in Utah (Beck, 1990), which is about half as far as has been previously reported for individuals in Nevada (Gienger, 2003). Movement metrics (movement frequency, average distance traveled per movement, and cumulative distance traveled per active season) were consistent within individuals but differed across years. Year influenced all movement metrics at sites A and C and within each population, a specific subset of years seemed to drive most of the annual variation in movement patterns. At site A, metrics in 2001 and 2002 were consistently different than the same metrics in 2003 and 2004. At site C, 2018 metrics consistently varied from those in 2021. Although there is notable variability in movement patterns, it is concentrated within specific years and does not translate to long-term variability in overall space use.

Data deficiency persists as an obstacle to conservation, and long-term studies on Gila monster spatial ecology have not explored both intra- and inter-annual space use simultaneously. Reported estimates of the species' space use have used estimation methods or sampling regimes that are inadequate for capturing long-term movement patterns. Thus, biologically relevant and temporally appropriate information is needed to inform long-term management goals (Wildlife Action Plan Team, 2012). This study, which was replicated across sites,
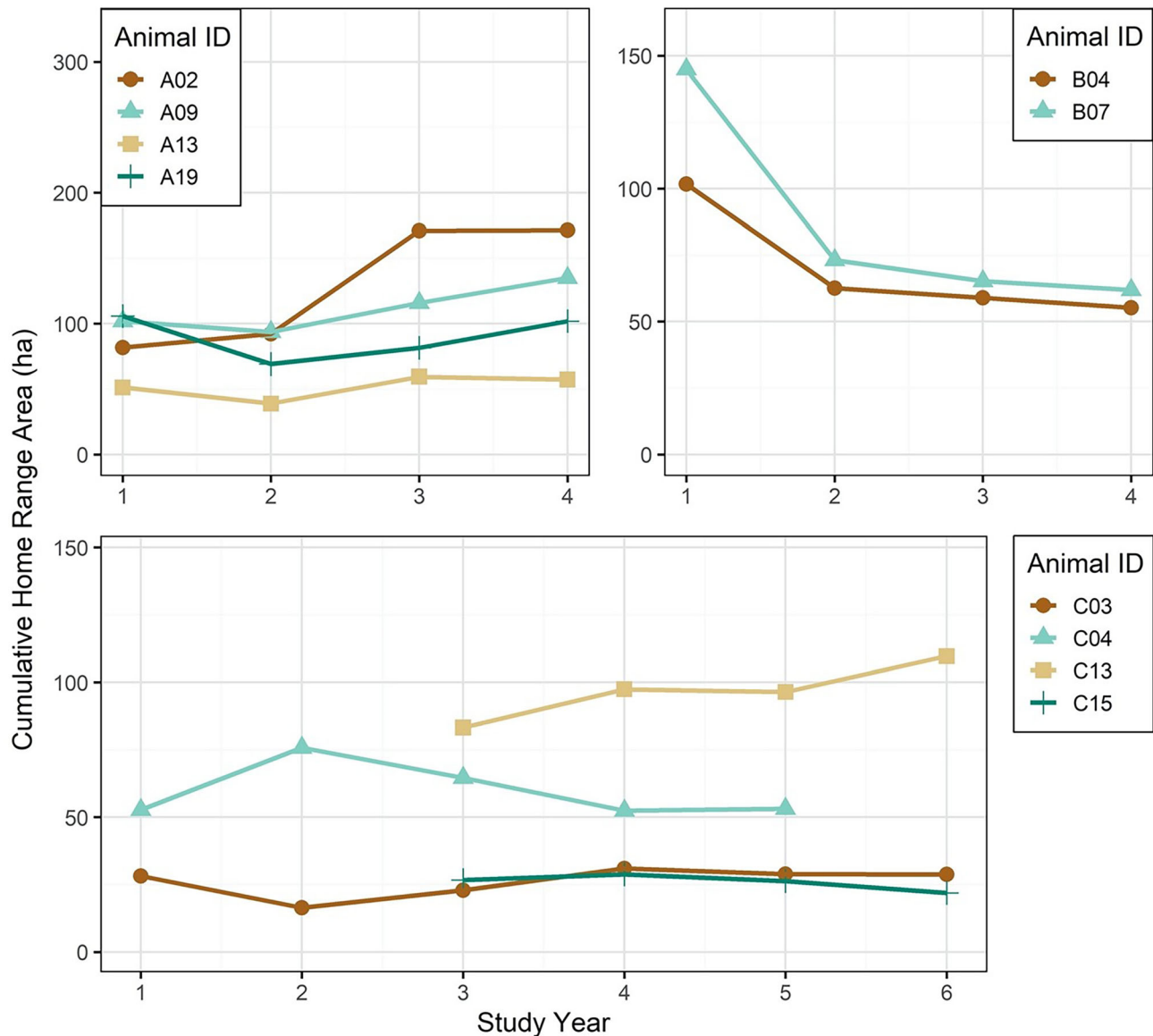
Figure 6 Variability in cumulative home range size over time of the longest-tracked individuals from three populations of Gila monsters (*Heloderma suspectum*) in southern Nevada tracked between 2001 and 2021. Home range size was calculated with area-corrected autocorrelated kernel density estimation (AKDE).

accounts for autocorrelation, and has relatively large sample sizes, contextualizes population-level movement patterns within the unique spatial ecology of the species. We found that while Gila monsters modify their movement patterns year to year, they have high site fidelity, and home range size is consistent (repeatable) across years, possibly due to the species' reliance on familiar thermal refuge sites. Similarly, other research has found that Gila monsters exhibit high fidelity even in urbanized areas, increasing their risk of road mortality (Kwiatkowski et al., 2008). Extreme site fidelity (i.e., high fidelity that does not vary based on habitat quality/availability) may be maladaptive in the face of anthropogenic disturbance and can have

genetic and energetic consequences that reduce population viability (Matthiopoulos et al., 2005; Merkle et al., 2015). For example, the amount of genetic diversity (and adaptive potential) within a population is shaped by local population size and connectivity with other populations through dispersal and gene flow (Wright, 1931). Genetic diversity will decline with population size reductions and increased isolation through genetic drift, increased inbreeding, and reduced gene flow (Schlaepfer et al., 2018). We found no indication of dispersal in adults but did observe dispersal in one subadult. Juvenile dispersal may increase gene flow and settlement of suitable habitats. Future investigations exploring dispersal and habitat selection of

juveniles could provide insight into their role in population connectivity. Research into the specific environmental drivers for the patterns we observed, especially that which addresses resource/habitat selection and the fine-scale movement patterns of Gila monsters may also help to elucidate the spatial strategies and/or behavioral adaptations that allow the species to endure extreme environmental variation.

Author contributions

JBS, JLJ, and CMG conceived the ideas, designed methodology, and collected the data; JBS analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of cumulative home range (HR) size estimates for Gila monsters (*Heloderma suspectum*) in southern Nevada. Estimates were calculated using area-corrected autocorrelated kernel density estimation (AKDE) with and without optimal weights.

Table S2. Summary of annual home range (HR) size estimates for Gila monsters (*Heloderma suspectum*) in southern Nevada. Estimates were calculated using optimally weighted area-corrected autocorrelated kernel density estimation (AKDE).