

Resource Subsidies Alter Spatial Ecology of Gila Monsters

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ABSTRACT: Resource subsidies can have profound effects on animal behavior, reproduction, and growth. Resource subsidies often result from human-altered environments that augment natural resources, creating small-scale enriched landscapes (“terrestrial islands”) juxtaposed with less productive natural landscapes. Effects of artificially enriched landscapes can be more pronounced in arid-land systems where resource availability is already limited. We analyzed patterns of space use and movement of Gila Monsters (*Heloderma suspectum*) based on radio telemetry data from a subsidized resource (water and prey) environment (Stone Canyon Golf Club) and compared them to individuals from a natural environment (Owl Head Buttes). After adjusting estimates of area use for sex, number of relocations, and year, males in the subsidized resource environment had a mean home range area (minimum convex polygon) of 13.6 ha (range: 4.4 – 24.0 ha), while females had mean home ranges of 8.3 ha (2.0 – 35.8 ha). In the natural environment, males had an average home range area of 43.2 ha (21.5 – 82.7 ha) while females had an area of 23.6 ha (7.9 – 47.6). Gila Monsters from the two environments exhibited seasonal differences in movement patterns, primarily between the dry and monsoon seasons, with home ranges in the subsidized environment being smaller (13.0 ha for males, 10.5 ha for females) and slightly more stable than home ranges in the natural environment (23.7 ha for males, 23.6 ha for females). To explore spatial arrangements within and between sexes, we examined overlap of home range areas. There were differences in home range overlap within and between sexes; in the subsidized population, there was very little male-male overlap (only two occurrences), but a high degree of female-female overlap (7 occurrences). In the natural population, there was very little female-female overlap (one occurrence) but a high degree of male-male overlap (7 occurrences), likely because home ranges were approximately twice as large in the natural population. Male home ranges extensively overlapped female home ranges at

both sites. Gila Monster home ranges may be smaller and packed more densely together in subsidized resource environments than those of natural environments due to increases in available resources.

Key Words: *Heloderma*; Home range; Reptile conservation; Resource subsidies

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INTRODUCTION

ORGANISMS, nutrients, and resources may often cross the boundaries of adjoining ecosystems. Movement of materials and nutrients, often subsidizing environments across ecotones and environmental borders is frequently studied in the context of food web dynamics (Anderson and Polis 2004; Polis et al. 1998; Sabo and Power 2002a,b). Studies of resource subsidies, such as increased water input and availability of food reveal changes in distribution, growth, and relative abundance of both consumers and producers as a function of resource availability, and these changes may have cascading effects across food webs (Anderson and Polis 1999; Newsome et al. 2013; Polis et al. 1997; Polis and Hurd 1995). In resource-limited systems, resource subsidies can substantially alter processes governing life history traits, abundance, density, behavior and distribution patterns of individuals (Marczak et al. 2007; Newsome et al. 2013; Polis and Hurd 1995; Sabo and Power 2002). Some of the most important subsidized terrestrial ecosystems, such as greenways, gardens, and golf courses, are found in desert regions, created by artificial water sources (i.e. irrigation). Given that primary productivity in natural terrestrial ecosystems is largely a function of precipitation (Ludwig 1986; Polis 1991; Sponseller et al. 2012), increases in plant-available moisture from artificial sources may substantially alter the prey base available to desert species at higher trophic levels (Forkner and Hunter, 2000; Oksanen et al. 1981). This results in increased available resources which are readily exploited by habitat occupants (Boarman et al. 2006; Newsome et al. 2013).

A key question in ecology is how the spatial patterns of individuals are influenced by the distribution and availability of resources (Börger, et al., 2006 a, b; Lima and Zollner 1996; Matthiopoulos 2003; Wiegand et al. 1999). Spatial patterns are a complex function of behavioral decisions related to resource availability and are influenced by temporal and individual-level

mechanisms (Anderson et al. 2005; Börger et al. 2006b; McLaughlin and Ferguson 2000; Murrell and Law 2000; Tufto et al. 1996). Therefore, alterations to the environment that affect resource distribution and availability can have profound consequences on activity and spatial pattern. Anthropogenic alterations, such as horticulture, and irrigation can supplement nutritional and water resources available to some wildlife, resulting in increased survival and altered daily activity levels (Altman and Muruthi 1988; Atwood et al. 2004; Bino et al. 2010).

A common framework used to quantify spatial habitat use is the home range concept, defined as the area traversed by an individual during normal routine activities of survival and reproduction (Burt 1943). Routine movements may include behaviors such as seeking critical resources (e.g., food and water), reproduction (e.g., mate searching and nest site selection), and refuge selection. These behaviors may vary temporally with seasonal changes in the predictability of resources, and those of unpredictable disturbance events (Wingfield 2005). Therefore, the magnitude and consistency of individual spatial patterns may vary as a function of resource availability and distribution.

Carnivorous lizards typically have large home ranges due primarily to low availability and sparse distribution of prey resources (Guarino 2002; Nilsen, Herfindal and Linnell 2005; Christian and Waldschmidt 1984). A good example is the Gila Monster (*Heloderma suspectum*), a widely foraging nest predator that feeds almost exclusively on nestlings and eggs of small vertebrates (Beck 2005; Gienger and Tracy 2008 a,b). This somewhat specialized diet means that prey items are patchily distributed in time and space, and potentially unavailable outside of the nesting season of prey. This makes Gila Monsters a good focal species for studying potential changes to spatial habitat use that may result from resource subsidies. By quantifying spatial habitat use of Gila Monsters as a response to a resource-subsidized environment, we

hypothesized that space use is influenced by the distribution and availability of resources and we tested the prediction that Gila Monsters have reduced home range sizes in habitats with increased availability of resources (water and prey). We also expected that seasonal home range size is influenced by the temporal availability of resources, and if so, Gila Monsters occupying a subsidized environment should exhibit reduced variation in seasonal home range size in response to sustained seasonal resource availability, such as nesting prey and water access.

MATERIALS AND METHODS

Study Sites

We used radio telemetry to track Gila Monsters at two sites with contrasting levels of resource availability. The resource-subsidized population was at Stone Canyon Golf Club (Pima County, Arizona), where we tracked 22 individuals (13 females and 9 males) from 2007 – 2013. The site encompassed ca. 345 ha of typical Arizona Upland Sonoran Desertscrub (Brown 1994). Elevation ranged from 900 m – 1000 m. This site consists of a housing development with residential properties interspersed throughout the golf course. The landscape was characterized by granitic rock outcrops, interrupted by a network of watered turfgrass, ponds, and a paved cart path. A unique feature of Stone Canyon is that the design of the development is incorporated into the natural landscape (including vegetation and geological features) rather than large-scale leveling and clearing of areas for fairways and greens, which is a common practice in golf course design (Jackson et al. 2011).

For comparison, we tracked 15 Gila Monsters (6 males, 6 females and 3 sub-adults of unknown sex) from 2000 – 2002 from a natural population near Owl Head Buttes, ca. 19 km northeast of Stone Canyon (Gallardo 2003). Owl Head Buttes encompassed ca. 200 hectares, with an elevation range of 800 m – 900 m, and discontinuous rocky buttes throughout. Owl Head

had no urban development or other human-altered features other than a sparse network of unpaved dirt roads.

Season Categorization

We categorized seasons based on criteria that were ecologically relevant to Gila Monsters and comparable to other studies of these lizards (Beck 1990; Beck and Jennings 2003). We identified five distinct “seasons” to characterize activity patterns: winter, emergence, dry, monsoon, and post-monsoon. We characterized winter as a sustained interval of inactivity while sheltered in overwintering refugia, which are typically burrows within rocky buttes or outcrops in close proximity to an animal’s range of activity. Emergence is marked by the initiation of basking and surface activity after hibernation, with infrequent forays over short distances before returning to hibernacula (Beck 1990; Gienger 2003; Lowe et al. 1986). We considered the end of emergence season to be when movements increased in frequency and distance away from hibernacula; such movements signal the initiation of seasonal foraging and breeding activities (Beck 1990; Gienger 2003; Jones 1983; Lardner 1969). Emergence ranged from March 13 – April 16. The dry season encompassed the period between emergence and the onset of the summer monsoon season. Due to annual variation in the onset of monsoonal rains, the dry season was conditionally considered to begin April 17. However, because of considerable annual variation in the onset of the summer rains (Xu et al. 2004), we determined the start of the monsoon based on National Oceanic and Atmospheric Administration (NOAA) adjusted monsoon dates, which begin on the first day in which the average dew point temperature was greater than 12.7°C across three consecutive days; we considered the monsoon season to end on September 30 (Guido 2009; Mohrle 2003). The post-monsoon season typically has relatively stable climatic activity (e.g., temperature and precipitation), and we considered it extending from

the end of the monsoon season into the winter months when Gila Monster activity ceased, and lizards occupied winter hibernacula (October 1 – December 14).

Radio-Telemetry

We captured Gila Monsters during active day and night searching efforts and transported them to a lab where radio-transmitters were surgically implanted using the modified techniques of Reinert and Cundall (1982). Lizards were anesthetized and implanted intracoelomically with 13 g radio-transmitters (SI-2T Holohil Systems, Ltd., Ontario, Canada). Lizards were released at the site of capture after 48 hours of recovery post-surgery and tracked using a radio receiver (R1000 receivers, Communication Specialists) with a RA-23K antenna (Telonics, Mesa, Arizona). Tracking frequency varied from 3 – 5 days/week during the dry and monsoon seasons, and 1 – 2 days/week during the emergent and post-monsoon seasons when individuals are less active. We collected a mean of 2 fixes/day (range: 1 – 11), and recorded relocations using a handheld Global Positioning System using the Universal Transverse Mercator coordinate system.

Home Range and Home Range Overlap

We calculated home ranges using 100% and 95% Minimum Convex Polygons (MCP) (Jennrich and Turner 1969; Mohr 1947), and 95% Kernel Density Estimations (KDE) using the reference bandwidth (Börger et al. 2006a,b; De Solla et al. 1999; Worton 1989) implemented in the *adehabitatHR* package (Calenge 2006). We used the *ref* bandwidth as a conservative method for calculating kernel area estimates, because it has been shown to have reduced sensitivity to smaller sample sizes (Blundell et al. 2001). Home range estimation techniques can be sensitive to sample size (number of relocations), and the distribution of relocations (Blundell et al. 2001; Seaman et al. 1999; Worton 1995). Therefore, we used 100% MCP methods to calculate seasonal home range estimates to maintain the largest sample size possible during shorter time

intervals (seasons). To minimize temporal autocorrelation in estimates (Cushman et al. 2005; De Solla 1999), we only included relocations (whether the animal moved or not) separated by 24 h in analyses.

To investigate spatial arrangement and relationships within and between sexes, we used three methods to analyze home range overlap (Haenel et al. 2003). First, using 100% MCPs we calculated the number of overlapping male and female home ranges. Second, we calculated total home range area (ha) shared with other individuals, regardless of sex. If three or more polygons overlapped in a given area, we calculated that area as if it were the union of two polygons to avoid overestimation of shared area. Third, we calculated the proportion of the home range that was shared with other individuals.

We used Normalized Difference Vegetation Index (NDVI) to compare relative differences in primary productivity between sites. NDVI is defined as the fraction of measured photosynthetically active radiation absorbed by plants (Sellers 1985) and is often used as a metric for measuring primary productivity (Running et al. 2000). This primary productivity can be used as a proxy for resource availability (water and prey) at our study sites. We used atmospheric corrected Landsat 8 OLI/TIRS level 1 tier 1 images downloaded from the U.S. Geological Survey's Earth Explorer database (<https://earthexplorer.usgs.gov/>, accessed 28 March 2020) for NDVI measurements of each site over a single year. To compare the areas of each study site equally while incorporating the study sites in their entirety, we clipped Landsat images measuring 1800 m x 2550 m. We examined NDVI of the subsidized site and the natural site with imagery taken during the June dry season, providing a reference for the time of year (dry summer) when we would expect to see the greatest difference in primary productivity between sites.

Data Analyses

We used a Generalized Linear Mixed Model (assuming a Gaussian distribution) to compare overall, annual, and seasonal differences in MCP (100%) and KDE (95%) home range size between subsidized and natural populations. To account for the extent of the home range potentially related to infrequent exploratory movements, we further used 95% MCPs. 95% MCPs exclude relocations that may be related to those movements that are not part of an animal's home range. We compared area estimates using sample size as a covariate and lizard ID as an individual-level random factor to account for repeated measures. We used Tukey *Post Hoc* tests for pairwise comparisons of marginal means to assess model-adjusted differences among groups. We reported all as mean \pm 1 standard error (SE) of the mean. We calculated effect sizes (d) between groups in pairwise comparisons as the standardized difference between group means \pm 1 SE.

RESULTS

NDVI

The standard scale of NDVI ranges between -1.0 and +1.0. Values closer to zero and decreasing to -1.0 typically indicate abiotic features, while increasing positive values indicate a greater amount of healthy vegetation. NDVI values in our study ranged from about 0.05 – 0.57 at the subsidized site (median = 0.15). Vegetation values ranging from about 0.2 – 0.57 were concentrated within and around turfgrass areas (tee boxes, fairways and green) of the golf course, and values decreased with increasing distance to those areas. The natural site had a much narrower range of values, ranging from about 0.05 – 0.18 (median = 0.11).

Home Range Comparisons

Cumulative home ranges differed between resource environments, with the natural site having an overall MCP (100%) home range three times larger than the subsidized site (mean = 10.9 ± 3.3 for subsidized and mean = 33.7 ± 5.5 for natural; Table 1, Fig. 1). Sample size positively influenced home range size for the 100% MCP estimation method ($F_{1, 52} = 18.71$, $P < 0.0001$), but did not have the same effect for the 95% MCP and 95% KDE methods (95% MCP: $F_{1, 37} = 1.04$, $P = 0.31$ and 95% KDE: $F_{1, 38} = 0.05$, $P = 0.81$).

Home ranges differed by sex for 95% MCP ($F_{1, 33} = 18.14$, $P = 0.0001$), 100% MCP ($F_{1, 24} = 15.92$, $P = 0.002$), and 95% KDE ($F_{1, 26} = 15.92$, $P = 0.0004$) estimators; males had overall home range areas about twice as large as females (Table 1). *Post-hoc* group comparisons of 100% MCPs indicated that males in the natural environment (mean = 40.9 ± 6.1) had home ranges three times larger than those of the subsidized males (mean = 13.4 ± 4.2) ($d = 27.5 \pm 9.1$; $t_{23} = 3.00$, $p = 0.003$, Table 1). Although the effect is not statistically clear, the females from the natural site (mean = 23.8 ± 6.0) had nearly three times the home range area of those from the subsidized site (mean = 8.2 ± 3.2) (100% MCP: $d = 15.4 \pm 8.7$; $t_{42} = 1.76$, $p = 0.08$; Table 1, Fig. 2). Within-sex comparisons of the 95% MCPs showed that female home range areas at the natural site were much larger than female home range areas at the subsidized site ($d = 17.6 \pm 5.6$; $t_{57} = 3.11$, $p = 0.002$; Table 1). Using the 95% MCP method, we found a 25% reduction in the home range extent of subsidized males compared (mean = 10.7 ± 2.6) to the 100% MCP method (mean = 13.4 ± 4.0), while there was a 31% reduction in female home range area (mean = 4.5 ± 2.4). Lizards at the natural site showed a similar pattern, with a 20% reduction in the male home range extent (mean = 4.2 ± 4.4), while those of females (mean = 22.1 ± 4.5) were reduced by 26%. 95% Kernel estimations for male (mean = 35.0 ± 3.3) and female home ranges (mean =

23.0 ± 1.8) at the subsidized site were 96% and 80% larger respectively than 100% MCP estimates, with an overall mean of 26.1 ± 1.7 ha (averaged across sex; Table 1). Because kernel methods use a statistical probabilistic approach, larger home range estimates using these methods are typical compared to MCP methods. At the natural site, male (mean = 68.3 ± 11.9) and female kernel estimations (mean = 36.8 ± 4.3) were 43.4% and 42.9% larger respectively than 100% MCP estimates with an overall mean of 56.0 ± 8.7 hectares (averaged across sex; Table 1).

Seasonal Home Ranges

Seasonal home range areas of subsidized individuals (100% MCPs) varied among seasons, but individuals largely used the same core areas (Fig. 5) across seasons. Seasonal home range areas varied between environments ($F_{1, 27} = 7.28$, $P = 0.01$; Table 2), with a significant interaction effect of environment and season ($F_{3, 69} = 6.43$, $P = 0.0006$), indicating that changes in seasonal home range size were dependent on environment. Sex alone did not account for variation in seasonal home range areas between environments, but there was a significant interaction effect of sex and season ($F_{3, 68} = 4.86$, $P = 0.003$). There was also an effect of sample size on seasonal home range variation ($F_{1, 72} = 7.48$, $P = 0.001$). Seasonal home range areas of the subsidized environment were relatively small throughout the active season, with the greatest increases by males during the dry season compared to females (Table 2). Females at the subsidized environment displayed similar home range sizes during the dry season (10.2 ± 2.4) and monsoon season (10.7 ± 2.6), while males exhibited a reduction in home range size during the same time period (Table 2, Fig. 3). Seasonal home range areas at the natural site increased for both sexes in both the dry and monsoon seasons, with male home ranges being approximately twice as large as females in the dry season, and slightly reduced in the monsoon season (Table 2, Fig. 3). A seasonal increase in female home range extent continued from the dry season into the

monsoon season (15.7 ± 3.9 and 23.0 ± 4.0 respectively; Fig. 3). For both populations, home ranges during the emergence and post-monsoon seasons were similarly small, marking the beginning and end of overwintering periods (Table 2, Fig. 3). *Post-hoc* analyses of the subsidized population indicated a seasonal difference in home range size between the dry season and post-monsoon season ($d = 7.2 \pm 2.6$; $t_{80} = 2.6$, $p = 0.04$; table 2). There were no differences detected between any other seasonal combination (Table 2, Fig. 3). The natural population exhibited no difference between emergence and post-monsoon home range sizes, or between the dry season and monsoon season (Table 2, Fig. 3). We also detected seasonal differences between emergence and both the dry season and monsoon season, as well as between the post-monsoon season and both the dry season and monsoon seasons (Table 2, Fig. 3).

Home Range Overlap

There was a high degree of home range overlap among individuals in the subsidized population (Table 3), but less overlap among males than females. Overlap occurrences were observed in only two pairs of male-male home ranges areas; M14-M69 (0.5 ha) and M119-M215 (19.5 ha), accounting for only 16% of total male home range area. Mean male-male overlap was 10.0 ± 5.5 hectares, mean female-female overlap was 4.3 ± 0.9 hectares, and a mean male-female overlap of 5.3 ± 1.8 hectares. On average, 65% of the total male home range area was shared with a female home range. Female-female home range overlap averaged 29% (7.3 ha) of their total home range area. In the natural population, where home ranges were much larger, there was considerable male-male home range overlap (Table 4), but negligible female-female overlap with a single occurrence between females 15 and 17 (0.03 ha). Most male home range areas overlapped with at least one other male, and a mean overlap of 18.9 ± 4.5 hectares accounted for

78% of their total home range area. Home range overlap between males and females had a mean of 13.0 ± 4.2 hectares, accounting for 16% of the total female home range area.

Home ranges of lizards in the subsidized environment appeared stable, with relatively strong annual fidelity to areas of use (Fig. 5). There was no effect of year detected across the study period for all three home range estimation methods (100% MCP: $F_{1, 67} = 0.32$, $P = 0.56$; 95% MCP: $F_{1, 36} = 1.07$, $P = 0.30$; 95% KDE: $F_{1, 34} = 0.81$, $P = 0.37$). An interaction of sex and environment for the 95% MCP method was detected ($F_{1, 33} = 3.96$, $P = 0.05$), but there appeared to be no interaction in either the 95% KDE or 100% MCP methods (95% KDE: $F_{1, 25} = 2.41$, $P = 0.13$ and 100% MCP: $F_{1, 25} = 3.46$, $P = 0.07$).

DISCUSSION

Home ranges of Gila Monsters in a natural environment were more than three times larger (33.9 ha, 100% MCP) than home ranges in a resource-subsidized environment (10.4 ha, 100% MCP). This supports the hypothesis that resource availability influences the spatial ecology of individuals in a resource-limited environment. Home ranges in the subsidized population were also much smaller than those previously described for natural populations in Nevada (64.2 ha), Utah (34.8 ha), and New Mexico (58.1 ha) (Beck 1990; Beck and Jennings 2003; Gienger 2003). However, it is unclear to what degree local environmental variation, study duration and sampling intensity influence this result (previous studies occurred in differing environments and ranged from single to multi-year investigations).

Home range sizes at the subsidized site were not only smaller, but also relatively stable across years (Fig. 1). This may be due to a more concentrated distribution of relocations for each lizard at this particular site due to relaxed environmental constraints, such as supplemental water and food availability, as well as potential artificial refugia (Kwiatkowski et al. 2008). It seems

likely that Gila Monsters at the subsidized site arrange themselves spatially in a way that allows for the acquisition of critical resources over a smaller area. In contrast, increased seasonal variability of movement and foraging bouts over longer distances at the natural site result in a larger and more variable distribution of relocations, and therefore larger home ranges. Both male and female Gila Monsters at the subsidized site had smaller home ranges than at the natural site (Table 3, Figs. 2 and 3). Males from the subsidized site had smaller mean home ranges than females at the natural site and male home ranges were only 3% larger than the home ranges of subsidized females (Table 1). Even though female home ranges within sites are smaller than those of males, male home range sizes at the subsidized site were about the same as female home ranges. This may be the result of easier access to females during the breeding months, as well as accessibility to food and water resources throughout the active season.

Key resources provided by golf courses and surrounding residential developments are dramatically increased water availability (primarily due to irrigation), nutrient supplementation (nitrogen and phosphorus from fertilizers), and landscaping of yards and road edges, all of which contribute to the formation of terrestrial islands of increased resource availability within resource-limited landscapes (Tanner and Gange 2005; Goode and Parker 2016). As a result, primary productivity is increased, along with densities of consumers that feed on vegetation (Charnov et al. 1976; Polis et al. 1997; Senft et al. 1987; Werner 1984), augmenting the base of the food web and causing a bottom-up trophic cascade in these terrestrial island-like environments (Polis, Anderson and Holt 1997).

Biomass of primary consumers is often positively correlated with productivity (East 1984; Nilsen et al. 2005). The NDVI values of the subsidized site indicate that there is a higher proportion of moderately to highly watered healthy vegetation, whereas the natural site contains

values more indicative of dry vegetation during the dry month of June (Fig. 8) when natural rainfall is typically sparse to absent. Due to a potential increase in the abundance and density of primary consumers, upon which Gila Monsters likely feed at the subsidized site (most likely cottontail rabbits; Bock et al 2006), spatial requirements, and foraging intensity are likely reduced. Animal home range sizes are known to decrease with the increased abundance of food resources (Carbone and Gittleman 2002; Guarino 2002; McLoughlin and Ferguson 2000; Nilsen et al. 2005).

Diet is an important predictor for home range size of carnivores (Gittleman and Harvey 1982). At the resource-subsidized site, where there is an increase in food abundance and water availability, Gila Monsters may not need to have large activity ranges for successful foraging bouts, as is typical of lizards in natural environments (Gienger et al. 2014; Gittleman and Harvey 1982; Guarino 2002). In natural environments, Gila Monsters may need to move relatively long distances in search of their preferred prey (avian and reptilian eggs and altricial mammalian nestlings) to meet their metabolic needs (Beck 1990; Gienger et al. 2014). Besides clear differences in productivity (NDVI) between sites, there is also anecdotal evidence of a higher abundance of prey species in subsidized environments (Bock et al 2006). Smith et al. (2010) suggested that as a potential result of high prey abundance, Gila Monsters at the subsidized site grew much faster than previously reported estimates from natural populations (Beck et al. 2005) and even grew faster than Gila Monsters kept in captivity. Human alterations to environments are typically thought to have negative consequences on wildlife populations (Marwick 2000; Terman 1997). However, we have demonstrated that in some cases, environmental modifications in the form of resource subsidies may have positive localized effects.

Seasonal home range sizes at the subsidized site were more stable throughout the active season in contrast to those at the natural site. The greatest degree of increase in seasonal home range size was found to be during the dry months, correlating with the breeding season of Gila Monsters (Table 2, Fig. 3). This increase was primary due to increased activity of males during this season, while females maintained relatively constant home range sizes from the dry season well into the summer monsoonal rains (Fig. 3). This same seasonal pattern during the hot dry months were also observed at the natural site, but on greater scale (Table 2, Fig. 3). During the transition from the dry months into the monsoon season at the natural site, there was a slight decrease in male home range size, while females exhibited a continued increase matching those of the males. The contrast between the two sites may be due to irrigation at the subsidized site. Water irrigation throughout the activity season provides continued water availability and increased resulting primary productivity, presumably leading to an increase in prey.

Some vertebrate animals are able to increase reproductive output in response to an increase in primary productivity associated with anthropogenic resource subsidies (Madsen 1974; Hefflefinger et al. 1999; Mills et al. 1989; Westmoreland 1986). For example, Mourning Doves (*Zenaida macroura*) are known to sustain breeding from late spring into the fall, with breeding attempts as frequent as every 30 days in places where their reproductive energy demands can be met (Mills et al. 1989; Westmoreland 1986). Gambel's Quail (*Callipepla gambelii*) are able to produce additional broods as late as August – September in areas with sustained water and food availability (Hefflefinger et al. 1999; Hungerford 1960). This is notably important in xeric environments such as the Sonoran Deserts, where rainfall is a limiting resource for primary productivity, and therefore primary and secondary consumers. With the

advantages afforded by anthropogenic subsidies, Mourning Dove and Gambel's Quail populations can be larger at human altered sites, such as golf courses.

Rainfall often elicits a strong seasonal increase in surface activity of Gila Monsters, during which time they may drink copious amounts of water (9% – 22% of their body weight) to maintain positive water balance (Davis and DeNardo 2009, Gienger et al. 2014). Hydrated lizards are presumably more active during the onset of the monsoon season than during the hot dry season because they can rely on increased water availability (Davis and DeNardo 2009). Specifically, Gila Monsters are able to benefit from increased water availability by drinking more and by maintaining urinary bladder water reserves more efficiently. In the subsidized environment, where water resources not solely related to rainfall are present, Gila Monsters can increase surface activity during the hot dry season. The subsidized site contains a network of sprinklers and drip irrigation that provide daily watering of the turfgrass and adjacent vegetation that comprises the “rough” or out-of-play areas of the golf course. In addition, runoff from the golf course provides additional off-course water sources. These systems provide a sustained source of water to Gila Monsters throughout their entire active season, a luxury that is not afforded to the natural population.

We found contrasting patterns of home range overlap between males and females from subsidized and natural sites. Home range overlap among males from the subsidized site was minimal. In contrast, females exhibited greater home range overlap in the subsidized environment. These results differ from the natural population, where we documented extensive overlap among males. These contrasting patterns of shared space use may be attributed to both habitat structure, and availability of resources. Subsidized male Gila Monsters may benefit from the acquisition of food and mates over smaller areas, with subsidized females not being as widely

spaced as they are at the natural site. At the subsidized site, females are more closely oriented around the periphery of the golf course where there is a dense network of vegetation supporting prey and potential refugia. The degree of home range size and overlap within a species may be correlated with the abundance and predictability of nutritional resources within the habitat (McLoughlin et al. 2000; Vanek and Wasko 2017). Cost-benefit analyses suggest that the predictability and the abundance of food resources are important factors influencing animal territoriality, and therefore home range size (Maher and Lott 2000). Though Gila Monsters are not considered to be territorial, the same concept can be applied to animal home range size, and therefore to home range overlap.

There seems to be a higher density of Gila Monsters in the subsidized resource environment than has been noted for other natural populations (Beck 2005, Goode unpublished data). There may be a density-dependent effect on home range size as tighter packing of Gila Monsters in the resource subsidized site could reduce direct intraspecific competition, resulting in decreased individual home ranges. However, we observed an extensive network of home range overlap, particularly among females. If there were density-dependent effects, then we might expect a more reduced degree of home range overlap among individuals in order to avoid direct competition for resources. Our results do not support this idea of density dependence when we examine the degree of home range overlap, especially among females (Table 3).

Another important resource that can potentially influence space use is the availability of refugia. Beck and Jennings (2003) reported that Gila Monsters spent more time in areas with a higher density of shelters, and there was a tendency to use rocky shelter types more than mammal burrows due to their increased permanency. We could expect home range sizes to be altered with the availability and quality of refugia. With the addition of those resources playing

direct roles in nutritional requirements, interactions with the availability of refugia may further explain the complexities of spatial decisions. Due to the landscape structure of our subsidized site being largely intact, with minimal alterations to the natural landscape between and around greens with extensive rocky outcrops throughout, there may be a higher density of potential refuge sites available to Gila Monsters at the subsidized site.

Although our results lead us to conclude that Gila Monsters from the human-dominated environment appear to be faring better than their counterparts from a natural population, we remain concerned about Gila Monster populations subjected to potential negative effects of habitat fragmentation due to urbanization. Road systems may create barriers to movement both within and among populations, and lead to increased mortality rates, especially for more widely ranging males and, potentially, dispersing juveniles. This could very well be a contributor to the lower ratio of males to females radio tracked at our subsidized site. Habitat fragmentation in urbanized areas are known to cause behavioral changes in some species (Riley et al. 2003), as well as reductions in home range sizes due to limitations on movement, and in some cases, active avoidance of human altered areas completely, as Atwood et al. (2004) found with coyotes using suburban and rural environments. However, Kwiatkowski et al. (2008) found that moderate urbanization does not appear to have a major impact on Gila Monster home range size.

Reduction of Gila Monster home range size in resource-subsidized environments suggests that human-altered environments that provide resource subsidies to wildlife may have an array of consequences on spatial ecology. By gaining an understanding of the relationships among sex, foraging needs, spatial patterns, and distribution within differing environments, we can better manage wildlife populations through careful design of urban areas. These understandings may provide ways in which developers, state and federal agencies, and other

organizations can work together in recreational development, so that public benefit is accomplished, while simultaneously providing important conservation strategies to wildlife of concern affected by anthropogenic development.

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LITERATURE CITED

- Altman, J., and P. Muruthi. 1988. Differences in daily life between semiprovisioned and wild-feeding Baboons. *American Journal of Primatology*. 15:213–221.
- Anderson, D.J. 1982. The home range: a new non-parametric estimation technique. *Ecology*. 63:103–112.
- Anderson, W. B., and G. A. Polis. 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia*. 118:324–332.
- Anderson, W. B., and G. A. Polis. 2004. Allochthonous nutrient and food inputs: consequences for temporal stability. Pages 82–95 in G. A. Polis, M. E. Power, and G. R. Huxel, editors. *Food webs at the landscape level*. University of Chicago Press, Chicago, Illinois, USA.
- Anderson, D.P., J.D. Forester, M.G. Turner, J.L. Frair, E.H. Merrill, D. Fortin, J.S. Mao, and M.S. Boyce. 2005. Factors influencing female home range sizes in Elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecology*. 20:257–271.
- Atwood, T.C., H.P., H.P., and T.M. Gehring. 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. *Journal of Wildlife Management*. 68:1000–1009.
- Auffenberg, W., Q.N. Arain, and N. Khurshid. 1991. Preferred habitat, home-range and movement patterns of *Varanus bengalensis* in Southern Pakistan. *Mertensiella*. 2:7–28.
- Beck, D.D. 1990. Ecology and behavior of the Gila Monster in Southwest Utah. *Journal of Herpetology*. 24:54–68.
- Beck, D.D., and R.D. Jennings. 2003. Habitat use by Gila Monsters: the importance of shelters. *Herpetological Monographs*. 17:111–129.

- Beck, D.D. 2005. Biology of Gila Monsters and Beaded Lizards. University of California Press, USA. Pp.111–112
- Bino, G., A. Dolev, D. Yosha, A. Guter, R. King, D. Saltz and S. Kark. 2010. Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology*. 47:1262–1271.
- Blundell, G.M., J.A.K. Maier and E.M. Debevec. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs*. 71:469–489.
- Brito, J.C. 2003. Seasonal variation in movements, home range, and habitat use by male *Vipera latastei* in Northern Portugal. *Journal of Herpetology*. 37:155–160.
- Brown, D.E. 1994. Biotic communities of the Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City, USA.
- Brown, D.E. and Carmony, N.B. 1991. Gila Monster facts and folklore of America's Aztec lizard. Silver City, NM: High-Lonesome Books.
- Boarman, W.I., M.A. Patton, R.J. Camp, and S.J. Collins. 2006 Ecology of a population of subsidized predators: common ravens in the central Mojave Desert, California. *Journal of Arid Environments*. 67:248–261.
- Bock, C.E., E. Carl, Z.F. Jones and J.H. Bock. 2006. Abundance of Cottontail (*Sylvilagus*) in an exurbanizing southwestern savanna. *The Southwestern Naturalist*. 51:352–357.
- Börger, L., N. Reanconi, F. Ferretti, F. Meschi, G. De Michele, A. Ganze and T. Coulson. 2006a. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American Naturalist*. 168:471–485.

- Börger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari and T. Coulson. 2006b. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*. 75:1393–1405.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*. 24:346–347.
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modeling*. 197:516–519.
- Carbone, C. and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. *Science*. 295:2273–2276.
- Charnov EL, G.H. Orians, K. Hyatt. 1976. Ecological implications of resource depression. *The American Naturalist*. 110:247–259.
- Davis, J.R., and D.F. DeNardo. 2009. Water supplementation affects the behavioral and physiological ecology of Gila Monsters (*Heloderma suspectum*) in the Sonoran Desert. *Physiological and Biochemical Zoology*. 82:739–748.
- Davis, J.R. and D.F. DeNardo. 2010. Seasonal patterns of body condition, hydration state, and activity of Gila Monsters (*Heloderma suspectum*) at a Sonoran Desert site. *Journal of Herpetology*. 44: 83-93.
- De Solla, S.R., R. Bonduriansky and R.J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*. 68:221–234.
- Dunham, A.E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology*. 59:770–778.

- East, R. 1984. Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*. 22:245–270.
- Forkner, R.E. and M.D. Hunter. 2000. What goes up must come down? Nutrient addition and predation on oak herbivores. *Ecology*. 81:1588–1600.
- Gallardo, L.I. 2003. The role of thermal biology on home range ecology and refuge use in Gila Monsters. M.S. thesis. Arizona State University, USA.
- Gienger, C.M. and C.R. Tracy. 2003. Natural history of the Gila Monster in Nevada. M.S. thesis. University of Nevada, USA.
- Gienger, C.M. and C.R. Tracy. 2008a. Ecological interactions between Gila Monsters (*Heloderma suspectum*) and desert tortoises (*Gopherus agassizii*). *Southwestern Naturalist*. 53:265–268.
- Gienger, C.M. and C.R. Tracy. 2008b. *Heloderma suspectum* (Gila Monster) Prey. *Herpetological Review*. 39:224–226.
- Gienger, C.M., C.R. Tracy and K.A. Nagy. 2014. Life in the lizard slow lane: Gila Monsters have low rates of energy use and water flux. *Copeia*. 2:279–287.
- Gittleman, J.L. and P.H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology Sociobiology*. 10:57–63.
- Goldberg, S.R. and C.H. Lowe. 1997 Reproductive cycle of the Gila Monster, *Heloderma suspectum* in southern Arizona. *Journal of Herpetology*. 31:161–166.
- Goode, M., and M.R. Parker. 2016. Golf Courses. In: *Habitat Management Guidelines for Amphibians and Reptiles of the Southwestern United States*, Eds., L.L.C. Jones, R.L. Lovich, and K.J. Halama. *Partners in Amphibian and Reptile Conservation*, Technical Publication HMG-5.

- Guarino, F. 2001. Diet of a large carnivorous lizard, *Varanus varius*. *Wildlife Research*. 28:627–630.
- Guarino, F. 2002. Spatial ecology of a large carnivorous lizard, *Varanus varius* (Squamata: Varanidae). *Journal of Zoology*. 258:449–457.
- Guido, Z. 2009 Understanding the southwestern monsoon. *Southwest Climate Change Network: Feature Article*. <http://www.southwestclimatechange.org/feature-articles/southwest-monsoon>.
- Haenel, G.J., L.C. Smith and H.B. John-Alder. 2003. Home-range analysis in *Sceloporus undulatus* (Eastern Fence Lizard). I. Spacing pattern and the context of territorial behavior. *Copeia*. 1: 99–112.
- Heffelfinger, J.R., F.S. Guthery, R.J Olding, C.L. Cochran, Jr. and C.M. McMullen. 1999. Influence of precipitation timing and temperatures and reproduction of Gambel's quail. *The Journal of Wildlife Management*. 63:154–161.
- Huey, R.B., and E.R. Pianka. 1981 Ecological consequences of foraging mode. *Ecology* 62:991–999.
- Hungerford, C.R. 1960. The factors affecting the breeding of Gambel's quail *Lophortyx gambelii* in Arizona. Ph.D. dissertation, University of Arizona, USA.
- Huxel, G. R., K. McCann, and G. A. Polis. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. *Ecological Research* 17:419–432.
- Jackson, D.B., S.D. Kelly and R.D. Brown. 2011. Design guidelines for intergrading amphibian habitat into golf course landscapes. *Landscape and Urban Planning*. 103:156–165.

- Jennrich, R.I. and F.B. Turner. 1969. Measurement of non-circular home range. *Journal of Theoretical Biology*. 22:227–237.
- Jones, K.B. 1983. Movement patterns and foraging ecology of Gila Monsters (*Heloderma suspectum* Cope) in northwestern Arizona. *Herpetologica*. 39:247–253.
- Kelt, D.A. and D.H. Van Vuren. 2001. The ecology and macroecology of mammalian home range area. *American Naturalist*. 157:637–645.
- Kwiatkowski, M.A., G.W. Schuett, R.A. Repp, E.M. Nowak and B.K. Sullivan. 2008. Does urbanization influence the spatial ecology of Gila Monsters in the Sonoran Desert? *Journal of Zoology*. 276:350–375.
- Kokko, H. and B.B.M. Wong. 2007. What determines sex roles in mate searching? *Evolution*. 61:1162–1175.
- Lardner, P.J. 1969. Diurnal and seasonal locomotory activity in the Gila Monster, *Heloderma suspectum* Cope. Ph.D. dissertation, University of Arizona, USA.
- Lima, S.L., and P.A. Zollner, P.A. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*. 11:131–135.
- Lowe, C.H., C.R. Schwalbe and T.B. Johnson. 1986. The venomous reptiles of Arizona. Phoenix, AZ: Arizona Game and Fish Dept.
- Ludwig, J. 1986. Pattern and process in desert ecosystems, ed. Whitford, W. (Univ. of New Mexico Press, Albuquerque, NM), pp. 5-17.
- Mace, G.M. and P.H. Harvey. 1983. Energetic constraints on home-range size. *American Naturalist*. 121:120–132.
- Maher, C.R. and D.F. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. *The American Midland Naturalist*. 143:1–29.

- Marwick, M.C. 2000. Golf tourism development, stakeholders, differing discourses and alternative agendas: the case of Malta. *Tourism Management*. 21:515–524.
- Matthiopoulos, J. 2003. The use of space by animals as a function of accessibility and preference. *Ecological Modelling*. 159:239–268.
- McLoughlin, P.D. and S.H. Ferguson. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience*. 7:123–130.
- McLoughlin, P.D., S.H. Ferguson and F. Messier. 2000. Intraspecific variation in home range overlap with habitat quality: a comparison among brown bear populations. *Evolutionary Ecology*. 14:39–60.
- Mills, G.S., J.B. Dunning and J.M. Bates. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. *The Condor*. 91:416–428.
- Mitchell, M.S. 1997. Optimal home ranges: models and application to black bears. Dissertation. North Carolina State University, USA.
- Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. *The American Midland Naturalist*. 37:223–249.
- Mohrle, C.R. 2003. The southwest monsoon and the relation to fire occurrence. M.S. thesis. University of Nevada, USA.
- Morreale, S.J., J.W. Gibbons and J.D. Congdon. 1984. Significance of activity and movement in the Yellow-bellied slider turtle (*Pseudemys scripta*). *Canadian Journal of Zoology*. 62:1038–1042.
- Murrell, D. J. and R. Law. 2000. Beetles in fragmented woodlands: a formal framework for dynamics of movement in ecological landscapes. *Journal of Animal Ecology* 69:471–483.

- Newsome, T.M., G.A. Ballard, C.R. Dickman, P.J.S. Fleming and R. van de Ven. 2013. Home range, activity and sociality of top predator, the dingo: a test of the resource dispersion hypothesis. *Ecography*. 36:914–925.
- Newsome, T.M., J.A. Dellinger, C.R. Pavey, W.J. Ripple, C.R. Shores, A.J. Wirsing and Dickman. 2015. The ecological effects of providing resource subsidies to predators. *Global Ecology and Biogeography*. 24:1–11.
- Nilsen, E.B., I. Herfindal and J.D.C. Linnell. 2005. Can intra-specific variation carnivore home-range size be explained using remote-sensing estimates of environmental productivity. *Ecoscience*. 12:68–75.
- Notaro, M., Z. Liu, R.G. Gallimore, J.W. Williams, D. Gutzler and S.L. Collins. 2010. The complex seasonal cycle of ecohydrology in the Southwest United States. *Journal of Geophysical Research – Biogeosciences*, 115, G04034. doi:10.1029/2010JG001382.
- Oksanen, L., S.D. Fretwell, J. Arruda and P. Niemelä. 1981. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*. 118:240–261.
- Phillips, J.A. 1995. Movement patterns and density of *Varanus albigularis*. *Journal of Herpetology*. 29:407–416.
- Polis, G.A. 1991. The ecology of desert communities, ed. Polis, G.A. (Univ. of Arizona Press, Tucson, AZ), pp. 1-26.
- Polis, G.A. and S.D. Hurd. 1995. Extraordinary high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences*. 92:4382–4386.

- Polis, G.A., W.B. Anderson and R.D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*. 28:289–316.
- Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist*. 147:396–423.
- Polis, G. A., S. D. Hurd, T. C. Jackson and F. Sanchez-Pinero. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California islands. *Ecology*. 79:490–502.
- Porzer, L.M. 1981. Movement, behavior, and body temperature of the Gila Monster (*Heloderma suspectum*) in Queen Creek, Pinal County, AZ. M.S. thesis. Arizona State University, USA.
- Reinert, H.K. and D. Cundall. 1982. An Improved surgical implantation method for radio-tracking snakes. *Copeia*. 1982:702–705.
- Riley, S.P.D., R.M. Sauvajot, T.K. Fuller, E.C. York, D.A. Kamradt, C. Bromley and R.K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology*. 17:566–576.
- Rose, B. 1981. Factors affecting activity in *Sceloporus virgatus*. *Ecology* 62:706–716.
- Rose, B. 1982. Lizard home ranges: methodology and function. *Journal of Herpetology*. 16:253–269.
- Row, J.R. and G. Blouin-Demers. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia*. 2006:797–802.

- Ruby, D.E. 1976. The behavioral ecology of the viviparous lizard, *Sceloporus jarrovi*. Ph.D. Univ. of Michigan. 214 pp.
- Running, S.W., P.E. Thornton, R.R. Nemani and J.M. Glassy. 2000. Global terrestrial gross and net primary productivity from the Earth Observing System. In O. Sala, R. Jackson and H. Mooney (Eds.), *Methods in ecosystem science* (pp. 44–57). New York: Springer–Verlag.
- Sabo, J.L. and M.E. Power. 2002a. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology*. 83:1860–1869.
- Sabo, J.L. and M.E. Power. 2002b. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. *Ecology*. 83:3023–3036.
- Scott, R.L., W.J. Shuttleworth, T. O’Keefer and A.W. Warrick. 2000. Modeling multiyear observations of soil moisture recharge in the semiarid American Southwest. *Water Resources Research*. 36:2233–2247.
- Seaman, E.D., J.J. Millsaugh, B.J. Kernohan, G.C. Brundige, R.J. Kenneth and R.A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *The Journal of Wildlife Management*. 63:739–747.
- Secor, S.M. 1994. Ecological significance of movements and activity range for the Sidewinder, *Crotalus cerastes*. *Copeia*. 1994:631–645.
- Senft R.L., M.B. Coughenour, D.W. Bailey, L.R. Rittenhouse, O.E. Sala and D.M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience*. 37:789–99.
- Simon, C.A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. *Ecology*. 56:993–998.

- Smith, D.C. 1985. Home range and territory in the striped plateau lizard (*Sceloporus virgatus*). *Animal Behavior*. 33:417–427.
- Smith, J.J., M. Amarello and M. Goode. 2010. Seasonal growth of free-ranging Gila Monsters (*Heloderma suspectum*) in a Southern Arizona population. *Journal of Herpetology*. 44:484–488.
- Sponseller, R.A., S.J. Hall, D.P. Huber, N.B. Grimm, J.P. Kaye, C.M. Clark and S.L. Collins. 2012. Variation in monsoon precipitation drives spatial and temporal patterns of *Larrea tridentate* growth in the Sonoran Desert. *Functional Ecology*. 26:750–758.
- Stamps, J. and S. Tanaka. 1981. The influence of food and water on growth rates in a tropical lizard (*Anolis aeneus*). *Ecology*. 32:33–40.
- Stamps, J. 1994. Territorial behavior: testing the assumptions. *Advances in the Study of Behavior*. 23:173–237.
- Tanner, R.A. and A.C. Gange. 2005. Effects of golf courses on local biodiversity. *Landscape and Urban Planning*. 71:137–46.
- Taylor, E.N., M.A. Malway, S.V. Browning, S.V. Lemar and D.F. DeNardo. 2005. Effects of food supplementation on the physiological ecology of female Western diamond-backed rattlesnakes (*Crotalus atrox*). *Oecologia*. 144:206-213.
- Terman, M.R. 1997. Natural links: naturalistic golf courses as wildlife habitat. *Landscape and Urban Planning*. 38:183–197.
- Tufto, J., R. Andersen and J.D.C. Linnell. 1996. Habitat use and ecological correlates of home range size in a small cervid: the Roe deer. *Journal of Animal Ecology*. 65:715–724.

- Turner, F.B., R.I. Jennrich and J.D. Weintraub. 1969. Home ranges and body size of lizards. *Ecology*. 50:1076–1081.
- Vanek, J.P. and D.K. Wasko. 2017. Spatial ecology of the Eastern hog-nosed snake (*Heterodon platirhinos*) at the northeaster limit of its range. *Herpetological Conservation and Biology*. 12:109–118.
- Werner E, J. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*. 15:393–426.
- Westermoreland, D.A. 1989. The significance of clutch size, egg colorization, and other reproductive traits of Mourning doves. Ph.D. Dissertation, Iowa State University, USA.
- Wiegand, T., K.A. Moloney, J. Naves and F. Knauer. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *American Naturalist*. 154:605–627.
- Wingfield, J.C. 2005. The concept of allostasis: coping with a capricious environment. *Journal of Mammalogy*. 86:248–254.
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.
- Worton, B.J. 1995. A convex hull-based estimator of home range size. *Biometrics*. 51:1206–1215.
- Xu, J., X. Gau, J. Shuttleworth, S. Sorooshian and E. Small. 2004. Model climatology of the North American monsoon onset period during 1980–2001. *Journal of Climate*. 17:3892–3906.

TABLE 1. — Overall marginal means of male and female Gila Monster home range sizes (hectares +/- S.E.) across multiple years by estimation method from a natural site compared to a subsidized resource site in Arizona, USA.

Site	Sex	100% MCP		95% MCP		95% KDE	
		Mean	Range	Mean	Range	Mean	Range
Subsidized	Male	13.4 ± 4.0	4.4 – 25.0	10.7 ± 2.6	1.9 – 20.2	35.0 ± 3.3	14.5 – 55.2
	Female	8.2 ± 3.2	2.0 – 35.8	5.0 ± 2.0	1.3 – 16.7	23.0 ± 1.8	7.8 – 47.7
Natural	Male	43.5 ± 6.1	21.5 – 82.7	43.7 ± 4.2	15.3 – 68.4	68.3 ± 11.9	39.8 – 109.5
	Female	23.8 ± 6.0	7.9 – 47.6	21.8 ± 4.1	12.4 – 40.0	36.8 ± 4.3	26.4 – 51.8

TABLE 2.—Mean seasonal 100% MCP home range sizes of Gila Monsters (a. mean hectares +/- S.E.) of the natural and subsidized populations by sex for each population in Arizona, USA. Pairwise comparisons (b.) among seasons within each population after being averaged across sex with Tukey adjusted p-values.

Natural					Subsidized			
a.	Emergence	Dry	Monsoon	Post-Monsoon	Emergence	Dry	Monsoon	Post-Monsoon
Male	1.2 ± 0.8	29.5 ± 4.8	24.2 ± 3.7	0.3 ± 0.1	2.1 ± 0.9	18.3 ± 5.4	10.4 ± 2.4	0.6 ± 0.5
Female	4.5 ± 1.5	15.7 ± 3.9	23.0 ± 4.0	1.4 ± 0.7	2.1 ± 0.8	10.2 ± 2.4	10.7 ± 2.6	3.6 ± 1.7
Mean =	2.8 ± 1.0	23.7 ± 3.7	23.7 ± 2.6	0.7 ± 0.3	2.1 ± 0.5	13.0 ± 2.6	10.6 ± 1.8	3.0 ± 1.3
b. Pairwise								
Emergence	–	df = 69, t = 5.05, p = <0.0001*	df = 68, t = -6.36, p = <0.0001*	df = 73, t = 0.31, p = 0.98	–	df = 88, t = 2.54, p = 0.06	df = 89, t = -1.47, p = 0.45	df = 77, t = -0.26, p = 0.99
Dry	–	–	df = 67, t = -1.03, p = 0.72	df = 78, t = 5.09, p = <0.0001*	–	–	df = 66, t = 1.39, p = 0.50	df = 80, t = 2.66, p = 0.04*
Monsoon	–	–	–	df = 74, t = 6.42, p = <0.0001*	–	–	–	df = 84, t = 1.42, p = 0.48

TABLE 4.—Subsidized home range overlap of within and among sexes of Gila Monsters between individuals using 100%

MCPs. Male:Male overlap occurred in only two pairs of male home ranges, M14:M69 and M119:M215 at 0.5 and 19.5 ha respectively, and were therefore not included in the table. Net Overlap is total area contributing to overlap independent of that area shared by multiple lizards. Proportion is the proportion of overall home range area of individuals shared with other

lizards

ID	F36	F66	F104	F135	F137	F146	F147	M14	M67	M69	M112	M119	M215	M255
	<u>Male:Female</u>													
F36	-	5.13	-	-	-	4.65	-	-	-	-	-	19.44	18.51	-
F66	5.13	-	-	-	-	5.05	-	-	-	2.6	-	-	-	-
F104	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-
F114	-	-	-	-	-	-	-	-	-	-	5.82	-	-	-
F135	-	-	0.5	-	2.89	-	3.94	-	-	2.04	-	-	-	-
F137	-	-	-	2.89	-	-	7.91	-	-	0.55	-	-	-	-
F146	4.65	5.05	-	-	-	-	-	0.14	-	0.76	-	-	-	-
F147	-	-	-	3.94	7.91	-	-	3.73	0.21	4.6	-	-	-	-
F200	-	-	-	-	-	-	-	-	-	-	6.49	-	-	-
F252	-	-	-	-	-	-	-	-	-	-	-	-	-	3.45
Mean =	4.3 ± 0.86 S.E.							5.26 ± 1.78 S.E.						
ID	F36	F66	F104	F135	F137	F146	F147	M14	M67	M69	M112	M119	M215	M255
Net	7.13	7.05	0.5	4.44	7.91	7.36	8.96	3.97	0.21	6.7	12.31	19.44	18.51	3.45
Proportion	0.18	0.21	0.06	0.47	1	0.74	0.32	0.39	0.02	0.37	0.4	0.54	0.9	0.22

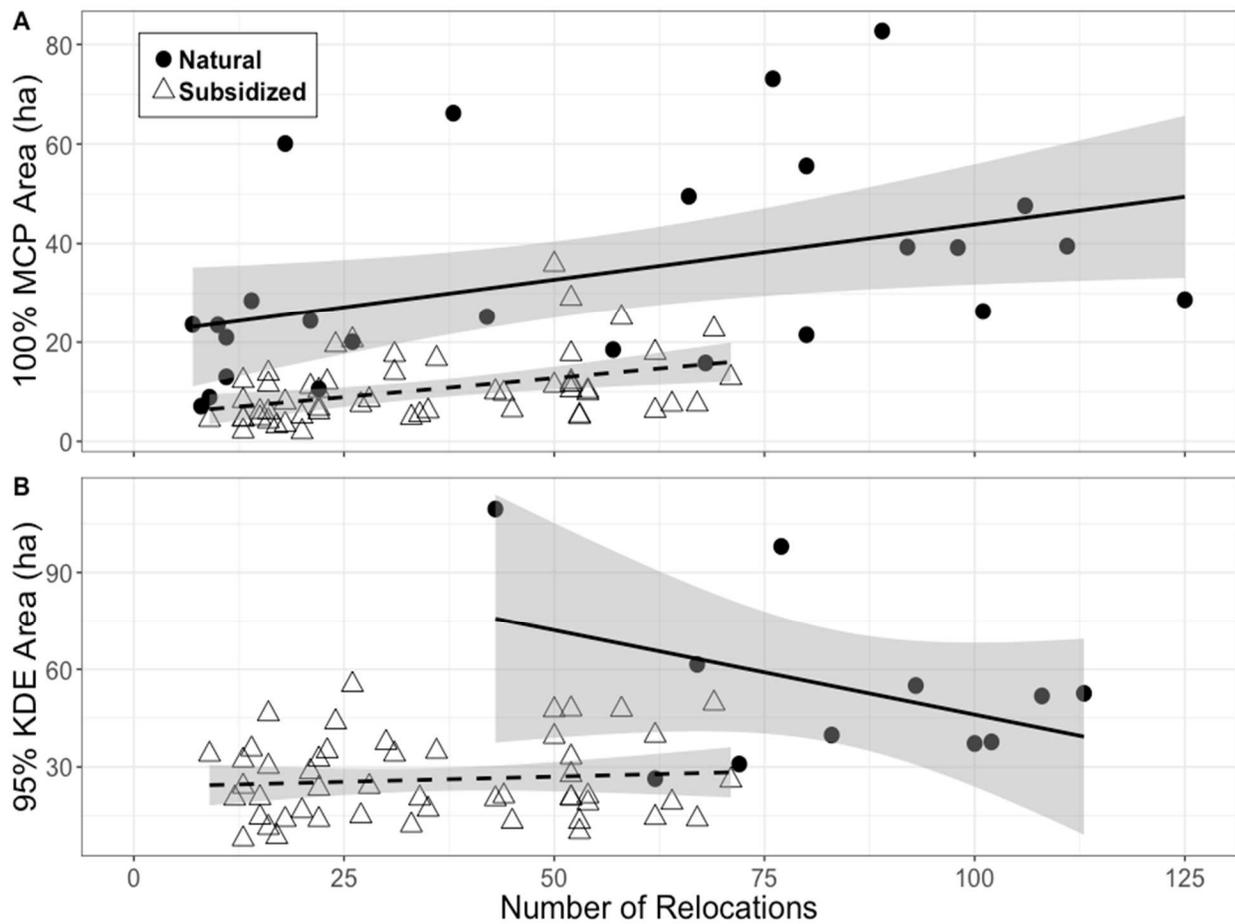


Fig. 1. —Gila Monster home range estimates plotted as a function of the number of relocations for resource-subsidized and natural populations. A. 100% MCP home range estimates. B. 95% KDE home range estimates.

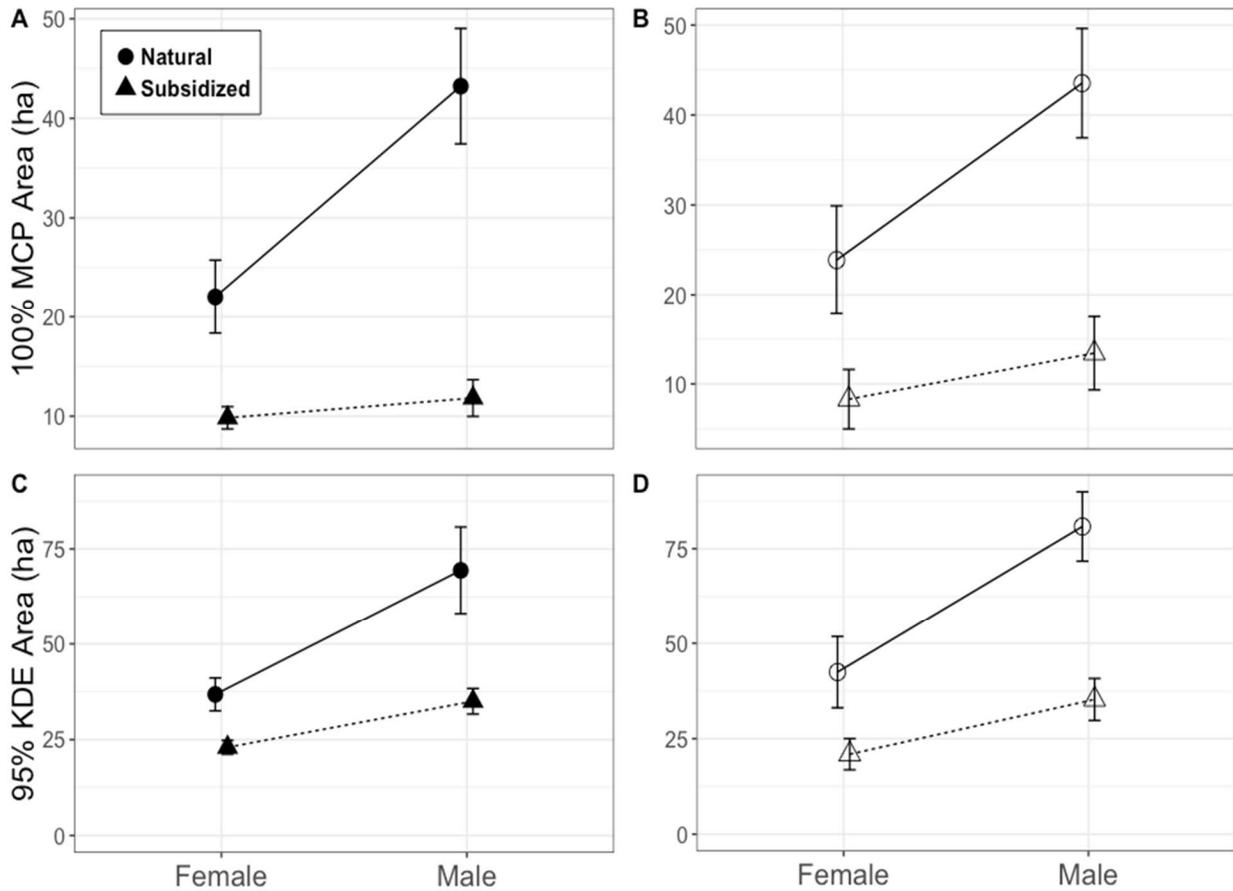


FIG. 2. —Means and marginal mean home range means (100% MCPs and 95% KDEs) for the subsidized and natural populations of Gila Monsters from the Sonoran Desert. Means were averaged across sex between each population. Filled symbols represent raw means and open symbols represent adjusted (marginal) means. A. Raw means, and B. Marginal mean home range estimates (100% MCP) after being adjusted for year, sex, and sample size. C. Raw means, and D. Marginal means for 95% KDE home ranges after being adjusted for year, sex, and sample size.

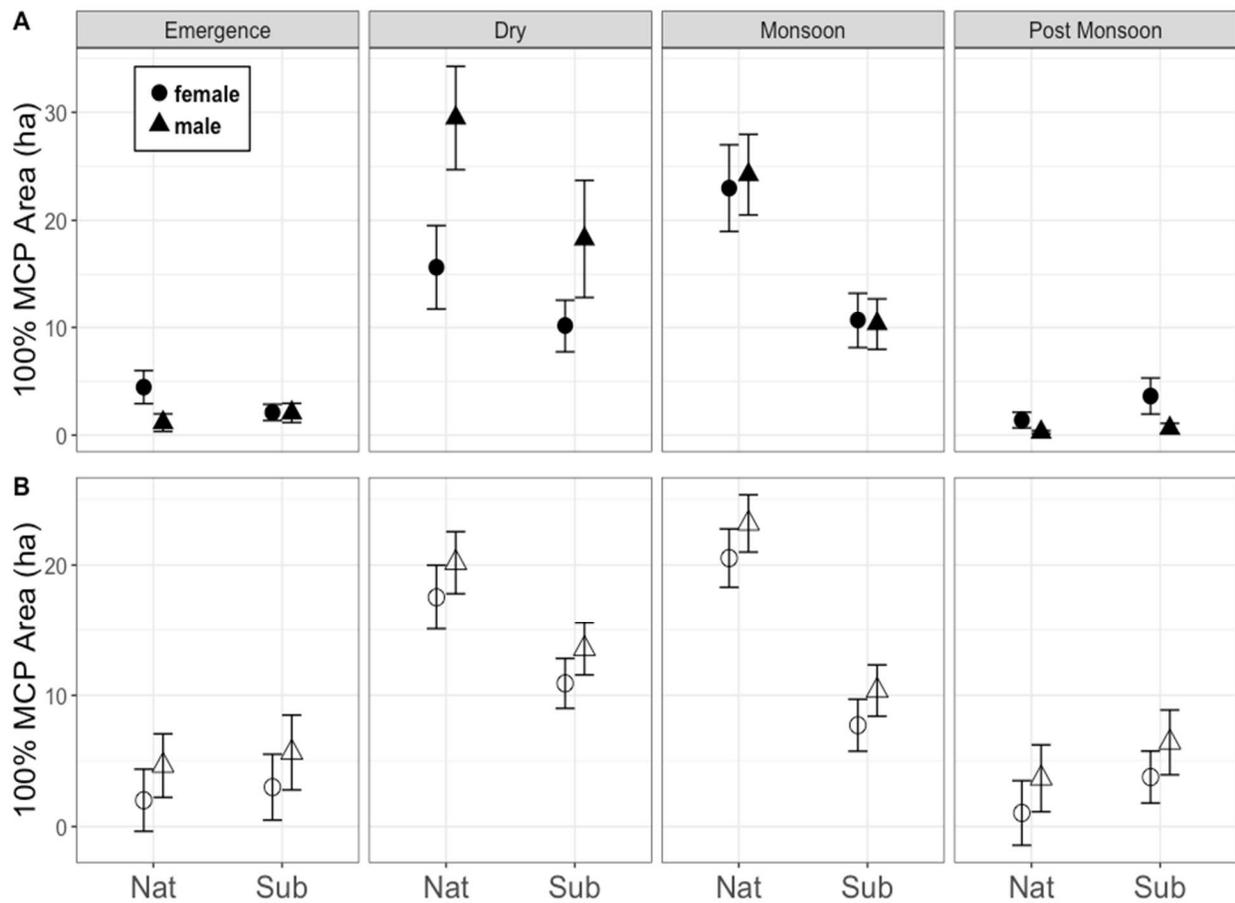


FIG. 3.—A. Mean 100% MCP home range estimates for each season between the subsidized and natural populations. B. Marginal mean home range estimates after being adjusted for year, sex, and sample size. Filled symbols represent raw means and open symbols represent adjusted means.

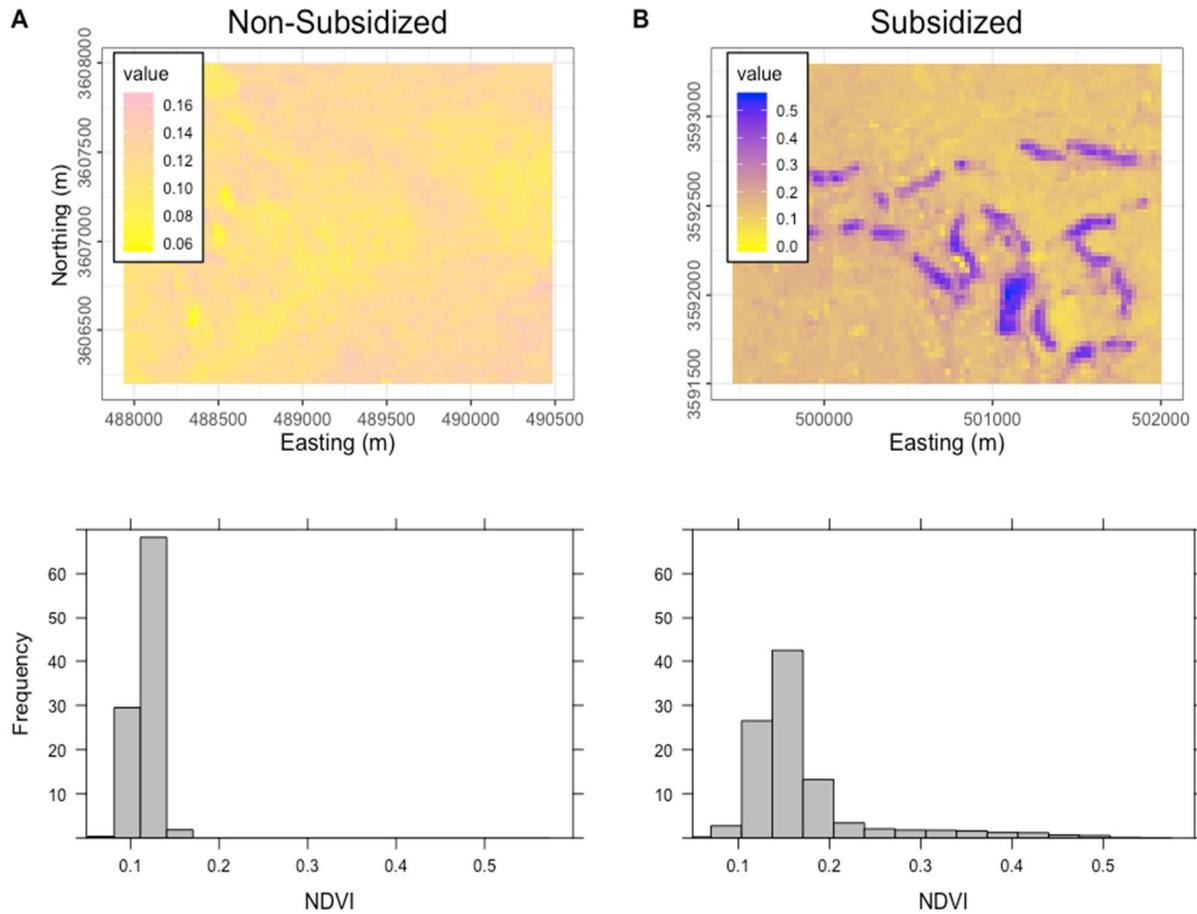


FIG. 8. — Images with corresponding histograms showing the distribution of NDVI values for each site. Each raster image depicts an area of 1800 m x 2550 m, and each pixel has a resolution of 30 m x 30 m. A; Natural environment. B; Subsidized environment. The scale of NDVI ranges between -1.0 and +1.0. Values near zero to -1.0 indicate abiotic landscape features while increasing positive values indicate increasing ‘green’ vegetation.

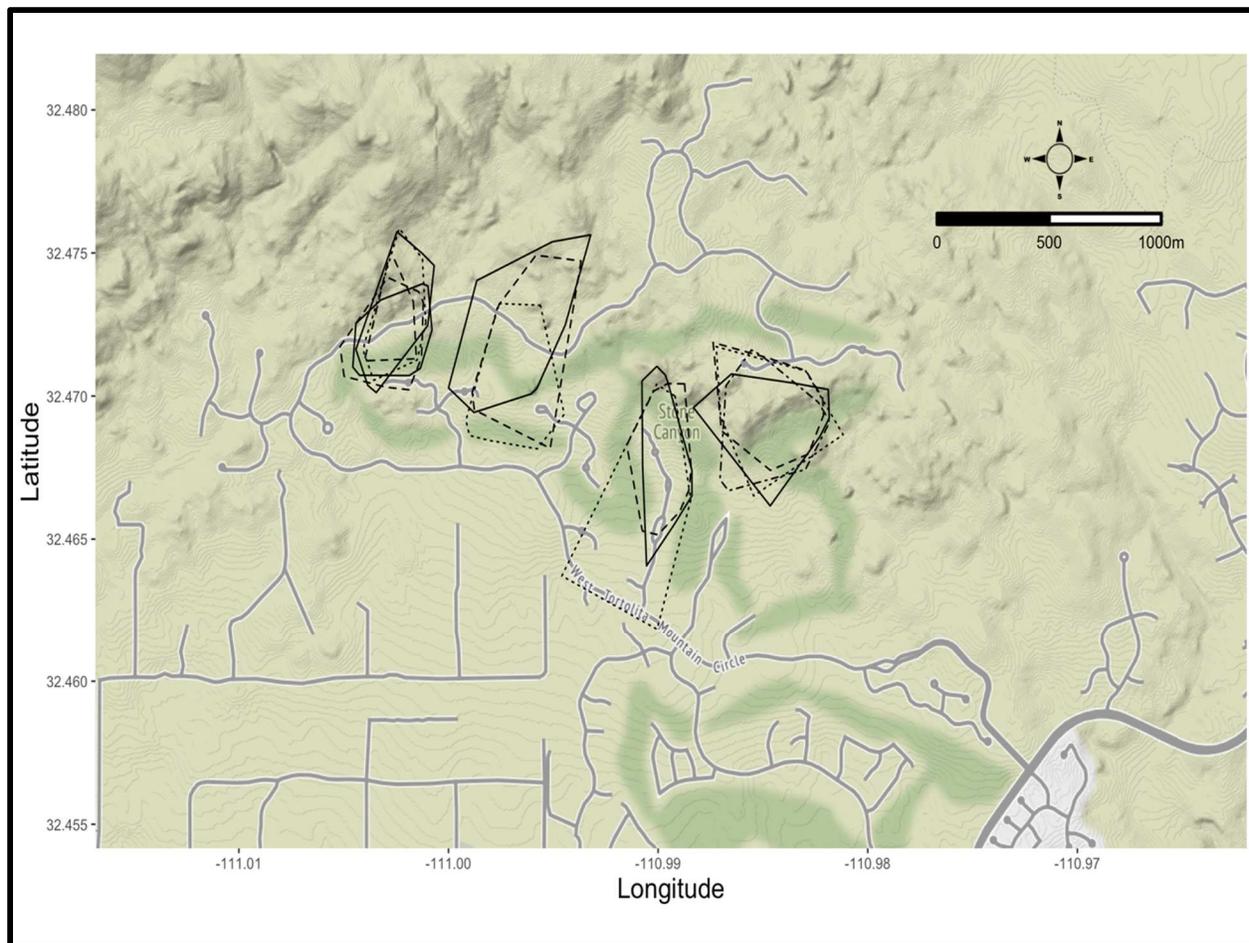


FIG. 4.—Typical yearly home ranges of four Gila monsters using 100% MCP estimates at the subsidized site. Each polygon represents one annual home range (home ranges did not shift appreciably among years of sampling). Bold grey lines represent major streets while the broad shaded regions represent the green fairways of the golf course.

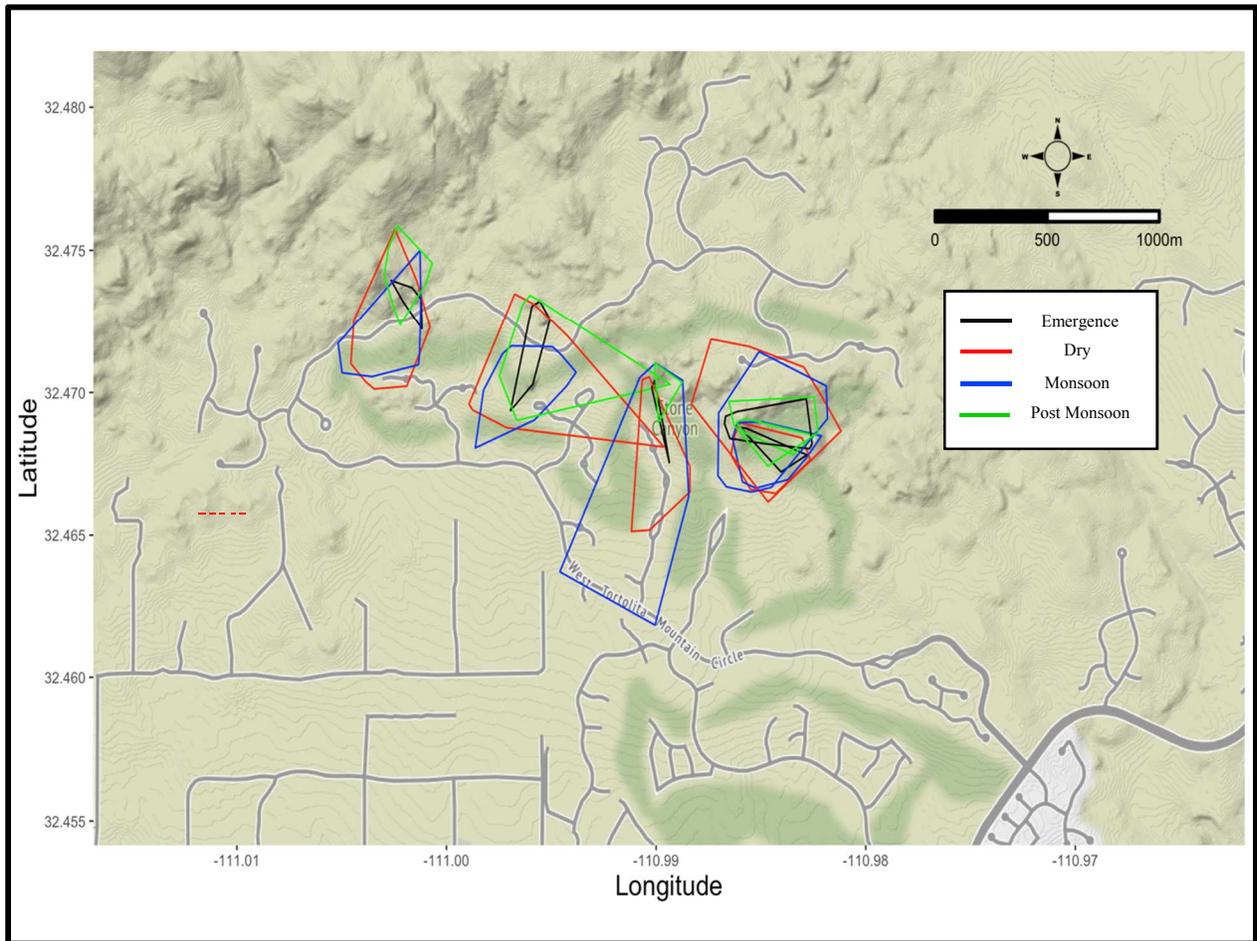


FIG. 5. —Seasonal home range polygons of Gila Monsters using 100% MCPs and pooled relocations from the entire study period. Home ranges of five individuals are shown by different line types used for each seasonal polygon and color coded according to each ecological season.

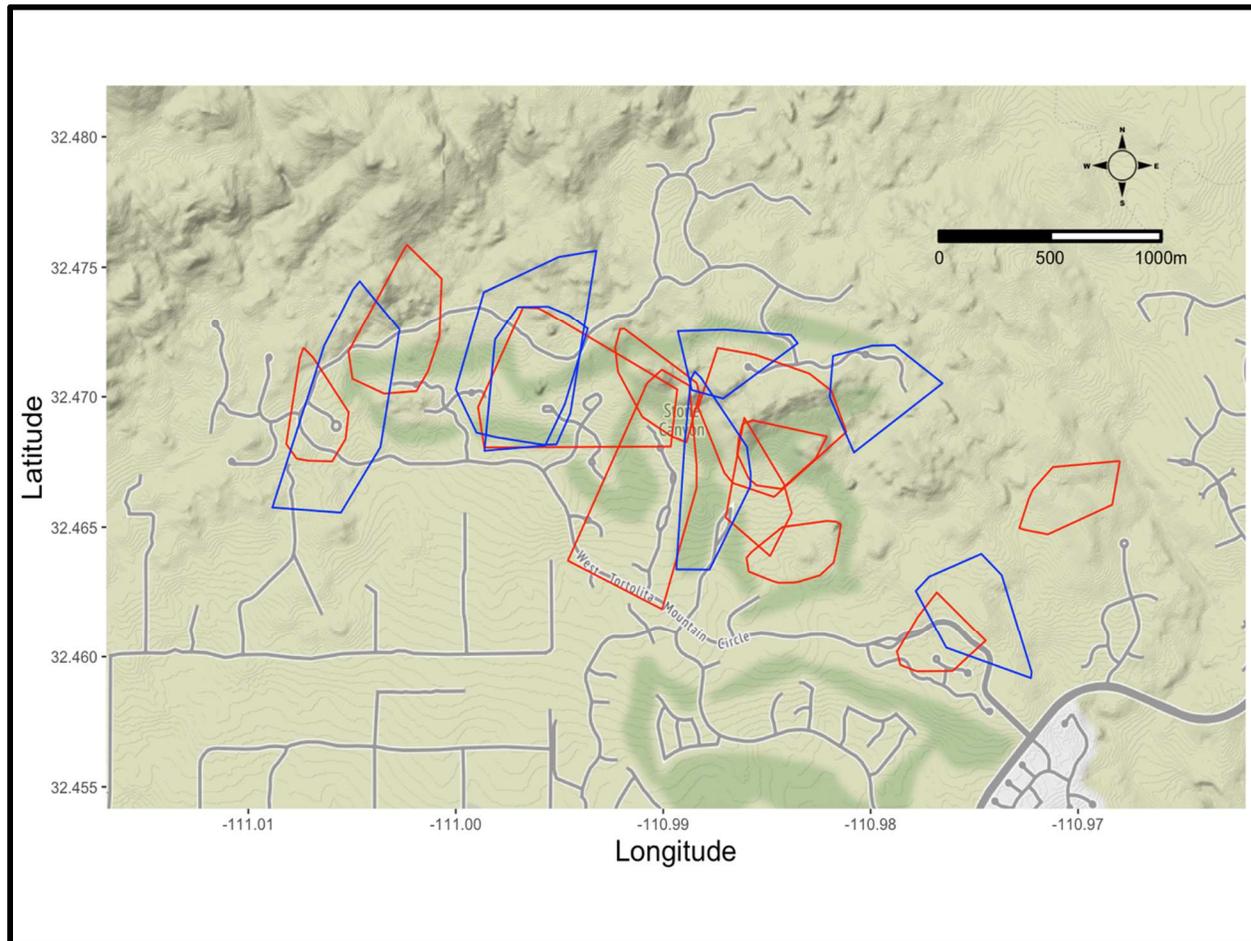


FIG. 6.—100% MCP home range polygons showing home range overlap of all male and female Gila Monsters at the subsidized site. Blue polygons represent male lizards and red polygons represent female lizards. Dark green shaded areas within and around polygons are golf greens and gray lines represent streets in and around the golf course.

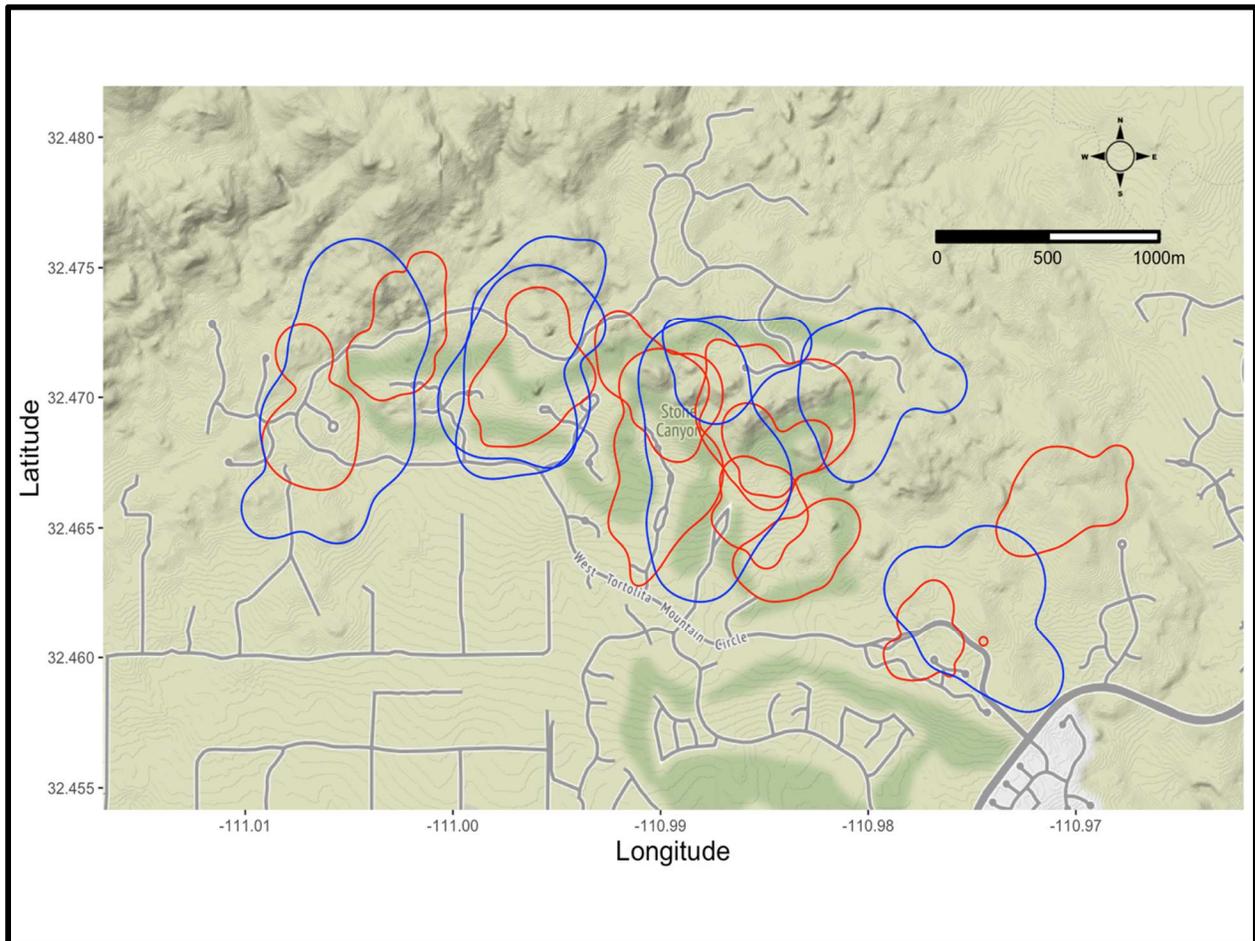


FIG. 7.—95% KDE home range polygons showing home range overlap of all male and female Gila Monsters at the subsidized site. Blue polygons represent male lizards and red polygons represent female lizards. Dark green shaded areas within and around polygons are golf greens, and gray lines represent streets in and around the golf course.