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A Long-term Study of Home Range of Coachella Fringe-Toed Lizards, *Uma inornata*

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ABSTRACT.— **Long-term field studies of relatively long-lived lizards can reveal environmental influences and ontogenetic responses over the lifetime of an individual that would not be apparent in data from short-term field studies. Hence, we initiated a long-term (31-yr) study of a population of the Coachella Fringe-Toed Lizard, *Uma inornata*, to determine demographic (sex, size/age, population density) and environmental (rainfall) influences on HR size of individuals. Mark-and-recapture data and observations on marked individuals provided sufficient sightings to estimate HR size using minimum convex polygons for 45 males and 40 females varying from age 0 (birth year) to age 5. Home range size was positively correlated with age and body size and was nonlinearly correlated with individual growth. Males grew faster and attained larger body size than did females and had larger HRs than did females of similar age. However, the mean body size–adjusted HR size for adult *U. inornata* did not differ significantly by sex. Home range size was inversely related to density in males but showed no relationship to density in females. There was a significant inverse relationship between HR size and winter rainfall preceding a field season. Within individuals, HRs shifted geographically and increased in size over sequential years as individuals grew. The location of an HR's centroid shifted between 4 and 62 m between years (mean 28 m for males, 15 m for females). Hence, combining HR data from multiple years will overestimate the actual spatial usage of an individual during any single year.**

The Coachella Fringe-Toed Lizard, *Uma inornata*, is endemic to aeolian sand habitats in the Coachella Valley of southern California. The habitat requirements of *Uma inornata* and its occurrence within the Coachella Valley are correlated with edaphic characteristics such as soil particle size distribution and compaction (Mosauer, 1932, 1935; Stebbins, 1943, 1944; Norris, 1958; Turner et al., 1984; Barrows et al., 2008). Urbanization and agricultural development drastically reduced the habitat and range of *U. inornata* (Turner et al., 1984) to such an extent that by 1980 only about 5% of its aeolian sand habitat remained, which placed the species in imminent danger of extinction. In 1980, *U. inornata* was listed as a Threatened Species by the United States Fish and Wildlife Service (US Department of the Interior, 1984) and as an Endangered Species by the California Department of Fish and Game (CESA, 1980). In 1986, the Secretary of Interior approved a Habitat Conservation Plan creating three preserves that constituted about 3,173 ha (The Nature Conservancy, 1985; Barrows, 1996). Additional habitat was preserved in 2008 when the Coachella Valley Multiple Species Habitat Conservation Plan subsumed the original 1986 preserves. Today there are at least five distinct populations remaining on an estimated 3,526–11,282 ha of protected habitat (Barrows et al., 2008; Vandergast et. al., 2016). Although the loss of 95% of *U. inornata* aeolian sand habitat was a major consideration for listing, little was known of its population biology. The scientific basis for listing the lizard relied mostly on laboratory and short-term field studies and inference from work on other phrynosomatid lizard species. Hence, in 1985, we initiated an ongoing long-term monitoring project to provide benchmark population biology data to inform management decisions on the preserves (Muth and Fisher, 1991).

The HR size of an animal integrates multiple population and environmental variables (Tinkle, 1967; Pechmann et al., 1991; Wake, 1994), and individual HR sizes are variable and dynamic within a population (Tinkle, 1967; Scoular et al., 2011). Long-term field studies are necessary to document and understand environmental influences and ontogenetic responses over the lifetimes of individuals. Knowledge of how HR size responds to environmental variations can provide insight into potential population-level responses to future environmental change and informed management practices (e.g., translocation or augmentation) when population responses fall outside of expected norms (Barrows et al., 2005). Here we synthesize information from the long-term field study to address the influence of population variables (sex, size and age, and population density) and environmental (rainfall) influences on HR size in *U. inornata*.

MATERIALS AND METHODS

Study Site.—Our study site is located in the Whitewater Floodplain Preserve (33.88° N, 116.52° W, datum WGS 84), Riverside County, California, near the city of Palm Springs. The site is a relatively flat, sandy floodplain that is sparsely vegetated with low shrubs. Barrows and Allen (2007) described the floodplain habitat as ephemeral sand fields; because of high winds, sand movement exceeds sand supply, depleting the available aeolian sand except where accretion dunes form under and leeward of shrubs (Fig. 1). The size of each accretion dune varies with the size and shape of individual shrubs and with the amount of aeolian sand available. Aeolian sand is replenished through episodic flood events that deposit fluvial sand upwind of the site. Vegetation is sparse overall at less than 8% cover, represented by two perennial shrubs: creosote bush (*Larrea tridentata*) and indigo bush (*Psorothamnus arborescens*); and three perennial subshrubs: California croton (*Croton californicus*), California scalebroom (*Lepidospartum squamatum*), and sandpaper plant (*Petalonyx thurberi*). An annual plant species that forms a subshrub, desert dicoria (*Dicoria canescens*), is common during normal or wet rainfall years but can be absent during drought years. An additional eight to ten species of annual plants occur on the site following good winter rainfall. *Uma inornata* either feeds directly on plant leaves, flowers, or both, or by eating arthropods that are associated with the plants (Durtsche, 1995).

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FIG. 1. The study site showing sparse vegetation and aeolian sand; lizards use the accretion dunes that form on the leeward side of vegetation. An adult female Coachella Fringe-Toed Lizard (*Uma inornata*) is shown in the inset.

The site receives about 135 mm of rainfall per year with nearly 80% occurring during the 6-mo period between November and April.

We established a 2.25-ha study plot within the site in the fall of 1984, superimposed on Plot 5 of Turner et al. (1984). We divided the 150 m × 150 m plot into a 10-m grid system and assigned an alphanumeric designation to the grid. Similar habitat extends well beyond the perimeter of the plot and thus it contains an open population of *U. inornata*.

Survey Protocol.—We surveyed the plot during the species activity seasons from 1985 through 2015. Surveys began in early March when adult lizards became active and ended in November or early December when declining temperatures triggered the cessation of their regular activity cycles. We attempted to survey the population on two nonconsecutive days of each week throughout the season, and such frequent sampling enabled us to reasonably census the population on our plot. We surveyed the plot in the morning when surface temperatures exceeded minimum voluntary body temperature (26°C; Brattstrom, 1965). Two observers walked parallel paths through each row of the grid. We also searched a 15-m buffer zone around the plot because the HR of some individuals was not fully contained within the plot boundaries. We surveyed the plot once per day (i.e., multiple passes were not made through the grid) and the time required to complete a survey varied from 3–6 h. If we observed an individual on more than one occasion during a survey, we used only the location of its first sighting. Our protocol minimized the effects that our activities might have had if we had, on subsequent movements, included multiple sightings of an individual during a survey. When we observed *U. inornata* under the canopy of vegetation, we gently tapped shrubs with lizard noose poles to induce the cryptic-colored lizards to move and thus be seen. In some cases, lizard footprints revealed their locations in sand or in burrows such that we could excavate them by hand. At the location where we first sighted an individual, we assigned alphanumeric coordinates relative to the nearest one or two grid points to an accuracy of ±1 m. Two of us (MF and AM) conducted all surveys as a team or, if one was absent, a trained field assistant substituted for him. Hence, there was continuity of personnel and field skill throughout the study.

The capture–recapture methods that we employed in our study required permanently marking all individual *U. inornata*. We toe-clipped (Medica et al., 1971) all individuals, limiting toe clips to the ungual phalanx to avoid damage to toe fringes, and attached colored beads to adults $\geq$60 mm snout–vent length (SVL) (Fisher and Muth, 1989). Colored beads enabled us to identify individuals without physically recapturing or otherwise disturbing them when resighted. We marked small individuals ($<$60 mm SVL) with a dorsal identification number using a black Sharpie® marking pen. We recaptured and remarked individuals after each shed until they attained the minimum beading size. After beading, we did not physically recapture individuals during a field season except to re-measure them once in the spring and again in the fall. When sighted, we recorded an individual's ID and location. If the animal was captured but unmarked, we determined its sex (Mayhew, 1965) and measured body length (SVL ± 1 mm) and mass (±0.1 g if <10 g, ±0.5 g if >10 g) with a clear plastic ruler and Pesola® spring scales, respectively. We also recorded tail condition, presence or absence of breeding color, injuries, and any noteworthy aberrations in coloration or scalation.

Home Range Estimation.—We use Burt's (1943) definition of home range (HR): "...that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as part of the home range." Our intent was to look at the extent, not the intensity, of space used by *U. inornata* (Worton, 1987). We followed the recommendation of Row and Blouin-Demers (2006) to use the minimum convex polygon (MCP) to calculate HR size for *U. inornata*.

We converted each alphanumeric sighting location to Universal Transverse Mercator (UTM) coordinates at a resolution of 1 m. We used ArcGIS version 10.2.1 (2014; Esri, Redlands, California) and Python scripting to calculate HR dimensions and display the results. ArcGIS provided the required spatial analysis tools for minimum convex polygon calculations and the cartographic tools for map production. We prepared our own Python scripts to flexibly select sets of observations for batch processing to MCP and 95% MCP, to save results in formats suitable as input to statistics applications, and to produce portable document format (PDF) map books showing results plotted on an aerial photo of the study area. We calculated full MCP areas for all sightings of an individual, for all sightings of an individual in a given year, and incrementally from the third through each additional sighting of an individual for a given year. Our incremental analysis of MCP size enabled us to verify that we had a sufficient number of sightings for the estimation of HR size for individuals (see below). We evaluated the efficacy of using a truncated MCP to reduce the variance in estimates of HR size, which could result in better statistical resolution. We calculated a 95% MCP by iterative removal of the sighting farthest from the polygon's centroid followed by recalculation of the centroid until 5% of the points were removed.

We used plots of HR size vs. number of sightings for each individual to determine whether each HR size was based on a sufficient number of sightings. Individuals whose HR size did not change appreciably with the addition of successive locations were used for HR analyses. As a consequence, our data set was limited to only those individuals with about 30 sightings for males, 25 for females, and 15 for juveniles.

To quantify potential ontogenetic shifts in HR geographic location among years, we calculated the centroid of the MCP polygon for the annual HR of all individuals that had sufficient sightings to calculate multiple annual HRs. We then measured the distance between centroids. For individuals that had more than two annual HRs, we averaged the distances between all centroids to lessen the influence of any single individual.

Age and Body Size, Sex, and Population Density.—An individual's body size varies over the course of a season, as younger individuals gain mass and length through growth while older individuals may lose mass as food resources diminish later in the year (MF and AM, pers. obs.). Because there is no good single measure of body size within a year for growing individuals, we incorporated the age–size relationship (see below; Fig. 2) into an analysis of HR size where age class serves as a proxy for body size. We used an analysis of variance (ANOVA) to analyze HR size separately by sex and a Bonferoni pairwise comparison to test the significance of differences among age groups. We inferred from Figure 2 that if HR size is positively correlated with age (body size), then it should exhibit a nonlinear asymptotic growth that is reflective of body size growth and, to test this, we fit the data to the logistic growth equation: $y = a/(1 + b/e^{(k^*x)})$, a special case of Richards' (1959) equation. Variables y and x are home range size (natural log transformed HR) and age, respectively; parameter a represents asymptotic HR size; b is related to size at age 0; k is an intrinsic growth rate; and e is Euler's constant. The estimate of parameter a should be slightly greater than the average adult HR size (Frazer et al., 1990) and thus would be good to report in HR studies for species where HR is shown to be affected by body size. We estimated parameters a, b, and k using an iterative Gauss-Newton method that computes exact derivatives using SYSTAT's nonlinear module (SYSTAT® 7.0, SPSS Inc.).

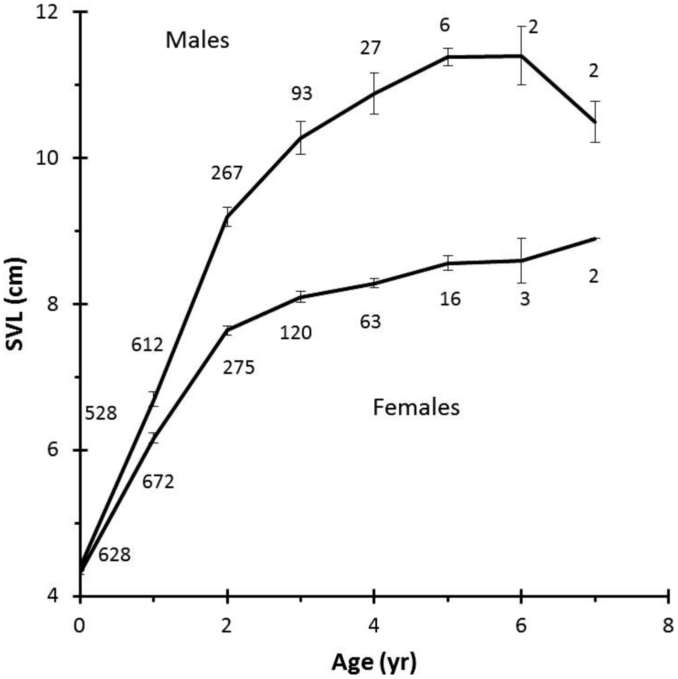

FIG. 2. Age-size relationship for the Coachella Fringe-Toed Lizard (*Uma inornata*) showing the mean length (SVL) at each age with sample sizes for all individuals measured during the study. Vertical bars are at 95% confidence interval (CI). Data include individuals that were measured multiple times during the study ($n = 3{,}316$).

In many lizard species, males are generally larger than females. Males usually have larger HRs, relative to their body sizes, than do females (Perry and Garland, 2002), with male and female HR size each scaling to SVL with an exponent of 1.8. Hence, we corrected for body size by dividing HR size by $\mathrm{SVL}^{1.8}$.

We looked for a relationship between adult density and adult HR size by regressing natural logarithm (Ln) HR against adult density. We used the number of individuals older than young-of-the-year that were recorded on the plot during a year as the number of adults for that year. That divided by the plot area, 2.25 ha, was considered to be the density.

Effect of Rainfall.—We used rainfall data from 1927–2015 (National Oceanic and Atmospheric Agency (NOAA), National Climatic Data Center: http://www.ncdc.noaa.gov/cdo-web/) from the Palm Springs airport located about 5.6 km SSE of the study site. We substituted the few missing rainfall data (most were zero rainfall that were not recorded) with data from a gauge that we installed at the study plot in 1985 or, for older missing data, from the University of California, Boyd Deep Canyon

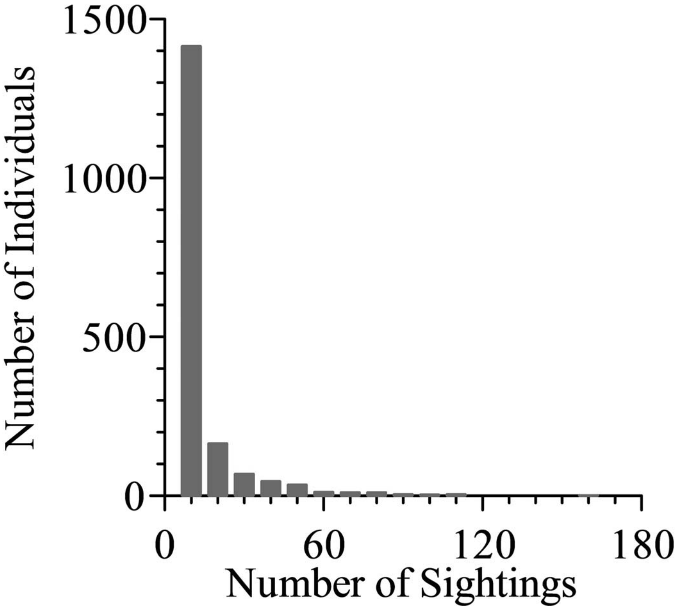

FIG. 3. Sighting frequency of all individual Coachella Fringe-Toed Lizards (*Uma inornata*) between 1985 and 2015.

Desert Research Center (http://deepcanyon.ucnrs.org). We calculated Standardized Precipitation Indices (SPI) using the method of McKee et al. (1993). An SPI is "spatially invariant" (Guttman, 1999) and therefore allows extrapolation to areas away from the data source because the magnitude of rainfall events in a region are similar even if the actual totals differ across the region. The SPI also contains a historical element in that standardized specific rainfall intervals using all of the specified intervals that were based on nearly 90 yr of data. We analyzed four interval lengths: 1) a 6-mo interval from November through April that encompassed the winter rainfall preceding a field season; 2) a 12-mo interval from July through June of the field season that added rainfall from the preceding summer; 3) an 18-mo interval through April of the field season including two winter rainfall periods plus the intervening summer rainfall; and 4) a 24-mo interval through June of the field season. The majority of precipitation from the 12-mo July through June interval falls prior to breeding, which begins in April or May (Mayhew, 1965). The study site contains perennial shrubs that serve as a food source either directly as leaves and flowers or indirectly as insects feeding on the shrubs (Durtsche, 1995). Because perennial shrubs might respond to longer interval lengths than 6 or 12 mo, we also analyzed 18- and 24-mo interval lengths. Treating each interval length independently, we summed rainfall within each interval for the entire rainfall record; e.g., the 6-mo interval length contained 90 values since 1927. Calculating SPI requires transforming these data. We determined that the Gamma 2 parameter (Pearson type III) probability distribution best fit the data using the method of Thom (1958) to estimate the two parameters. For interval lengths longer than one year, a log-normal distribution provides comparable fit to these data (see Angelidis et al., 2012), but for consistency we used the Pearson type III for all four interval lengths. We compared our SPI Index calculated for different time intervals by regressing Ln HR against SPI separately by sex. We used only individuals older than year one to reduce the influence of body size.

Statistical Procedures.—We used SYSTAT® 7.0 (SPSS Inc., 1997) for all statistical procedures using the $P = 0.05$ level of significance. Because residuals were not normally distributed, we used Ln transformations of HR.

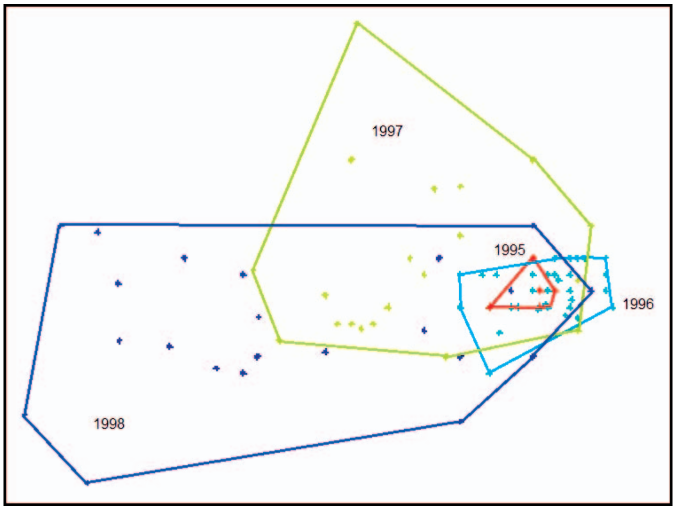

FIG. 4. Example of changes in HR size and location over the lifetime of an individual male Coachella Fringe-Toed Lizard (*U. inornata*) from the 1995 hatchling cohort.

RESULTS

Due to contingencies of weather and other logistical constraints in our multiple-year projects, the number of surveys varied from year to year (average 43, range 9 to 59). We surveyed the study plot 1,321 times during the 31-yr span and marked a total of 1,770 individuals. Their initial capture, plus 12,925 resightings, resulted in 14,695 total sightings on the plot. We resighted the majority of individuals infrequently; 80% $\leq$ 10 sightings each (Fig. 3). We sighted only about 20% of the known population on any given day. The individuals that went undetected during surveys likely moved in such a way as to avoid intersecting with our search path, were buried and inactive, or moved off the plot perimeter more than 15 m.

Of the 1,770 marked individuals, we could calculate home ranges for only 54 individuals (25 females, 29 males). However, we calculated multiple annual HRs for 21 of these individuals, resulting in 85 annual HRs for 40 females and 45 males. Annual home ranges of individual lizards revealed ontogenetic changes in size and shifts in location among years. An example of changes in HR over the lifetime of a male lizard is shown in Figure 4. The mean (standard error [SE]) shift in the location of the centroid among years is 14.6 m (4.4) for females and 28.0 m (5.4) for males, and overall the shifts ranged from 4 to 62 m. Thus, rather than HR increasing with age concentrically, most individuals shifted the location of their HR annually. An exception was a single female that shifted HR centroid a mean of 5.1 m (range 3.3–7.4) over six annual HRs. Had we estimated HR size by pooling sightings from multiple years, then the shifts demonstrated by most individuals coupled with the ontogenetic change in HR size (Fig. 5) would overestimate the HR area used by an individual in any particular year. Therefore, we treated each individual's annual HR independently.

95% vs. 100% Home Range Sizes.—The 95% HR did not decrease the variance of mean HR size, and the resulting shape of the distribution did not differ substantially as demonstrated by SD, G1, and G2 in Table 1. The 100% HR data fit the regressions of Ln HR vs. rainfall and vs. density better (higher r^2) than did

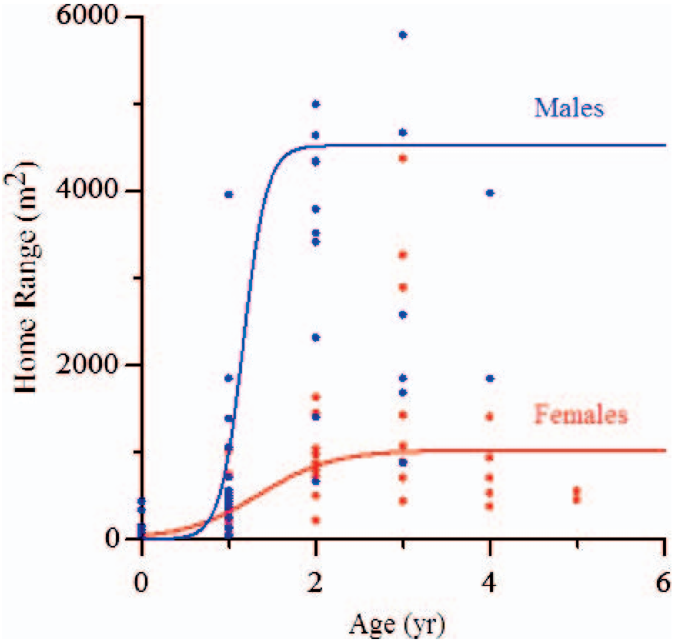

FIG. 5. Home range exhibits logistic growth over time for both sexes of Coachella Fringe-Toed Lizards (*U. inornata*). The asymptote estimated from a logistic growth equation is 1,025 m^2 for females and 4,523 m^2 for males.

the 95% HR. Likewise, the probabilities were comparable or better using 100% HR. Thus, we only report statistics from 100% HR henceforth.

Relationship between Home Range Size and Age, Body Size, and Sex.—The ANOVA of HR analyzed separately by sex revealed significant differences among age groups ($F_{5,\ 34} = 12.541$, $P < 0.0005$ for females; $F_{4,\ 41} = 23.979$, $P < 0.0005$ for males). A Bonferoni pairwise comparison indicated that the significance of the difference is lost among the older age groups; thus, we next performed an ANOVA on a subset of the youngest three age groups for each sex: ages 0, 1, and 2 yr, where young of the year comprise age 0 and again revealed significant differences: $F_{2,\ 21} = 16.758$, $P < 0.0005$ for females; $F_{2,\ 35} = 35.50$, $P < 0.0005$ for males. A matrix of Bonferoni pairwise probabilities reveals that, of the subset of home ranges for younger individuals, all age classes differ significantly ($P < 0.0005$ for all).

Home range size is positively correlated with age (body size; Fig. 2) and it is nonlinearly correlated with body size growth (Fig. 5). The logistic growth equation for HR of all females is $y = 6.932/(1 + 0.645/e^{1.267x})$; $r^2 = 0.585$. For all males, $y = 8.417/(1 + 0.943/e^{1.043x})$; $r^2 = 0.660$. A plot of these growth curves for both sexes exhibits asymptotic growth of HR as age increases (Fig. 5). The asymptotic parameter, *a*, is larger than the mean HR size of adults (Table 2). The mean body size-adjusted HR for adult *U. inornata*, using the size correction technique of Perry and Garland (2002), did not differ significantly by sex ($t = 1.136$, df $= 22$, $P = 0.268$). The mean size-corrected HR for adult males is 0.674 $m^2/mm^{1.8}$ and 0.456 $m^2/mm^{1.8}$ for adult females. Therefore, both sexes have the same body size : HR size relationship.

Effect of Rainfall.—The SPI for the 6-mo interval that encompasses winter rainfall at Palm Springs during the course of this study is given in Figure 6. The inverse relationship between rainfall and Ln HR is significant for both sexes at the 6-mo SPI interval (Table 3) but not at the other interval lengths. Removing the outliers from the male analyses, two with exceptionally large, and one with exceptionally small, HRs nearly tripled r^2. Rainfall from this 6-mo interval explains about 74% of the variation seen in male HR size and 26% in female HR size.

Effect of Density.—Annual adult density varied over the course of this study from 5.6 to 91.2 individuals per hectare (MF and AM, pers. obs.). We regressed Ln HR vs. adult density. For females, $y = -0.010x + 7.36$, $n = 25$, $r^2 = 0.059$, $P = 0.244$. For males, one outlier was identified, a male with an exceptionally small HR. Excluding that outlier gave the equation, $y = -0.016x + 8.70$, $n = 18$, $r^2 = 0.444$, $P = 0.003$. Thus, adult density has no significant effect on HR size of females but has an inverse relationship that explains about 44% of the variation in the HR size of males. Intuitively, it might seem that density and rainfall are correlated. However, there was no significant correlation between adult density and SPI for the entire census period (Pearson correlation coefficient = 0.053, $n = 31$, $P = 0.775$).

DISCUSSION

A Coachella Fringe-Toed Lizard's HR is not static and multiple factors affect the size of an individual's HR over its lifetime. Home range changes in size and location among years and HR size is positively correlated with age (body size) (Fig. 2) and nonlinearly correlated with body size growth (Fig. 5). Population density of adults has no significant effect on HR size of females but has an inverse relationship with the HR size of males. Such biological factors affecting HR size are in turn influenced by the overarching environmental effect of rainfall.

TABLE 1. Descriptive statistics for Ln HR by sex in the Coachella Fringe-Toed Lizard (*Uma inornata*). Minimum, maximum, and mean values were back-transformed to square meters.

	All females, $n = 40$		All males, $n = 45$	
Descriptive statistic	95% HR	100% HR	95% HR	100% HR
HR (m^2)				
Minimum	14	39	9	24
Maximum	2,051	4,368	4,020	6,235
Mean	255	505	353	662
Ln HR				
Standard deviation	1.18	1.12	1.92	1.64
Variance	1.39	1.26	3.67	2.68
Coefficient of variance	0.21	0.18	0.32	0.25
Skewness	−0.63	−0.54	−0.69	−0.63
Standard error skewness	0.37	0.37	0.37	0.37
Kurtosis	0.24	−0.06	−0.78	−0.71
Standard error kurtosis	0.73	0.73	0.69	0.69

TABLE 2. Comparison of mean adult (age > 1 yr) HR sizes with asymptotic value derived from logistic growth curves by sex in the Coachella Fringe-Toed Lizard (*Uma inornata*). Area values were back-transformed to square meters from Ln HR. Asymptotic HR approximates the mean size of only the largest HRs.

	Males			Females		
Descriptor	Area (m^2)	*n*	95% CI	Area (m^2)	*n*	95% CI
Mean HR	2,819	19	2,074–3,831	903	25	679–1,202
Asymptote	4,523	45	1,600–12,797	1,025	40	651–1,612

Short term HR studies could not capture the dynamic environmental and population level responses evident in this long-term study.

Long-term field studies are a necessity to document and understand environmental influences and ontogenetic responses over the lifetime of an animal. Unfortunately, short-term field studies are the rule rather than the exception. Perry and Garland (2002) analyzed the effects of sex, body size, diet, habitat, and phylogeny on HR size and, in their Appendix A, they listed 489 entries containing information for one sex or age group that were studied in one population at one time: 91 entries did not report the duration of the study. Of the 397 entries that reported the duration of the study, only 12 studies were equal to or greater than 24 mo. Short-term field studies are insufficient to capture the environmental influences and population level responses of relatively long-lived species (Tinkle, 1979; Pechmann et al., 1991; Wake, 1994).

Uma inornata has a convex HR. Our data support Row and Blouin-Demers (2006) assertion that MCP is better for some herpetofauna than kernel methods that use Least Square Cross Validation to estimate a smoothing factor, especially for species that have high site fidelity. We can demonstrate the high site fidelity exhibited by this species by examining the one individual that we resighted most often. Of its 156 total sightings over 8 yr, only 55 represented discrete locations with 1–17 sightings at each location. Many of its sightings were located on different parts of the same dune or from different locations under the same creosote bush. We found that *U. inornata* choose repeatedly to use a dune-top vantage point or a particularly shady area under a shrub. The high site fidelity displayed by *U. inornata* is not because of physical limitations to the distance an individual can move. The maximum HR area that we estimated, 6,236 m^2, would have a diameter of about 90 m if it were a circle. Given the mean maximum velocity calculated for a congener, *Uma scoparia*, of 2.381 m/sec on flat sand (Carothers, 1986), it could traverse that 90 m diameter in under 40 sec. Assuming that a conservative walking velocity is about 1/10 of running velocity, it could traverse it in about 6.5 min, which was corroborated by our observations, albeit rarely, of individuals at opposite margins of their HR within the same day. Thus, an individual can physically cross its HR within an activity period, but instead typically reuses specific sites.

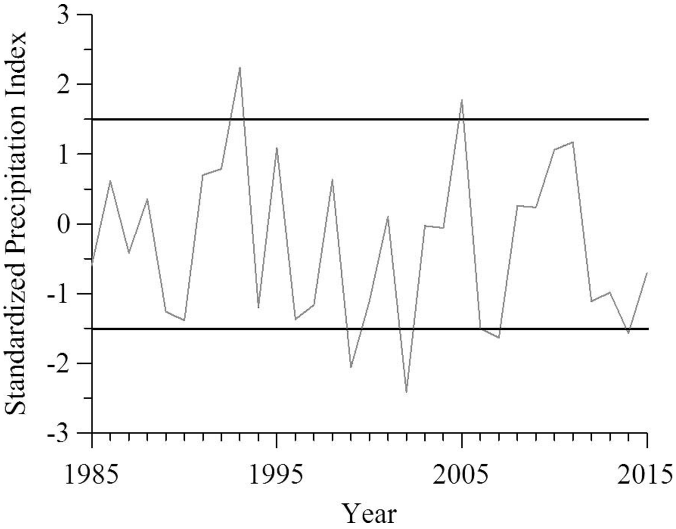

FIG. 6. Standardized Precipitation Index for the 6-mo interval that encompasses winter rainfall at Palm Springs during the course of the study. Rainfall intervals were standardized against all other November through April intervals since 1927/28. An index of 0 to −0.99 indicates mild drought, −1.00 to −1.49 moderate drought, −1.50 to −1.99 severe drought, and −2.00 to −3.00 extreme drought. Positive index values indicate wet years and horizontal lines designate severe drought-year and severe wet-year thresholds.

100% vs. 95% HR.—We evaluated the possibility that truncating Ln HR to 95% of its size will decrease the variance and enhance the shape (skewness and kurtosis) of the distribution of Ln HRs. Also, the probability of obtaining an actual 100% of locations is unlikely and thus 95% kernels are most often used to estimate utilization area (e.g., Powell, 2000). Our results show that, when using minimum convex polygons with this species, there is no benefit to using 95% Ln HR.

Home Range Size Varies by Sex, Age, Rainfall, and Density.—Few HR studies are of sufficient duration to capture among-year differences related to sex, size, and environmental variation. The difference between sexes in HR size that we observed appears to be related primarily to differences in body size. Both sexes are typical of most lizards in that they exhibit indeterminate growth (Hariharan et al., 2016). Female *U. inornata* grow more slowly than do males, and this disparity in body growth rates is evident during their first year of growth when mean body sizes begin to diverge significantly, albeit only 1 mm SVL and 0.1 g mass differences (MF and AM, unpubl. data). With the exception of the first year, when we detected no significant intersexual difference in HR size, we could not compare HRs of similar-sized or aged individuals between sexes because of the observed difference in growth rates between the sexes. Males grow faster and larger

TABLE 3. Regression statistics for Ln HR vs. SPI of multiple interval lengths in the Coachella Fringe-Toed Lizard (*Uma inornata*). We used HRs for individuals older than 1 yr to lessen the influence of body size, and three male outliers were excluded (see text).

SPI interval (months)	Slope		Constant		r^2		*P*	
	Females, $n = 25$	Males, $n = 16$	Females, $n = 25$	Males, $n = 16$	Females, $n = 25$	Males, $n = 16$	Females, $n = 25$	Males, $n = 16$
6	−0.31	−0.41	6.64	7.67	0.26	0.74	0.009	<0.0005
12	−0.09	0.10	6.79	8.01	0.03	0.03	0.437	0.486
18	−0.15	0.20	6.84	8.01	0.03	0.07	0.383	0.283
24	−0.30	−0.08	6.80	7.91	0.10	0.01	0.120	0.697

than do females and also have larger HRs than do females of similar-aged females. However, because growth becomes negligible in larger adults within a season, we were able to estimate body size for those older than year one. When we applied the size correction of Perry and Garland (2002) to these adults we found that, when scaled to body size, the HR area did not differ significantly between adult males and females. Thus, for this species in this population, females fit within the HR size/body-size continuum, although this is obscured by the difference in growth rates between sexes. A significant difference in the HR area of adult males and females is in contrast to most of the 160 species pairs analyzed by Perry and Garland (2002). We have no explanation for a lack of variation between the sexes unless it is related to the lack of either territoriality or within-sex aggression exhibited by this species. During 30 yr of working with *U. inornata* in the field, we never observed evidence of territoriality or intraspecific aggression, with two exceptions: 1) one act of cannibalism of a hatchling by an adult male, and 2) recent photographs (Heronema, pers. comm.) of two adult males engaged in an aggressive interaction similar to that illustrated by Carpenter (1963) of captive males. We believe that the photographed interaction was stimulated by the near proximity of a receptive female. To our knowledge, territoriality has never been demonstrated for *U. inornata* in a field study.

Our observed positive correlation between HR size and body size differs from the observations of Rose (1982) and Scoular et al. (2011) for findings on the Side-Blotched Lizard, *Uta stansburiana*. However, *U. inornata* is a much larger species that takes longer to reach adult size (Barrows and Fisher, 2009) and can better display the among-year, or within-season, differences that are relatively small in *U. stansburiana*. Growth of HRs is a logistic function related to body growth. We suggest that the asymptotic growth parameter, *a*, of the logistic growth equation can be used for comparisons among species or different populations within species, especially when using individuals of multiple sizes classes. As with body size (Frazer et al., 1990), the asymptotic value for HRs estimated for the population should lie just above the average adult HR size, as seen in Table 2. The difficulty in obtaining a sufficient sample size in multiple age–size groups, especially for the largest size classes, can affect the ability to confidently calculate asymptotic HR size, resulting in large confidence intervals. There is an apparent decline in HR size of the oldest age groups (Fig. 5) that may be a real effect of aging or instead may be that, because mortality is positively correlated with HR size, only individuals with smaller HR sizes survive to old age. The latter assumes that a larger HR increases the risk of predation. We do not have sufficient data to explore this further.

The hypothesis that metabolic needs influence HR size is supported by the inverse relationship between HR size and rainfall for both sexes. Assuming that food resources are limited during drier years, an individual must travel farther to secure enough food to meet its metabolic needs (Turner et al., 1969). Our data were limited by the paucity of rainy years during the study period. There were only 2 yr that had an SPI $\geq +1.5$ (Fig. 6), but during those years we collected sufficient data to calculate HR for only a single individual, a young-of-the-year male. Perhaps more data at the wet end of the rainfall spectrum would strengthen the inverse relationship between rainfall and HR size. Rainfall from the previous winter is the time interval that most influences HR. Although the study site is dominated by perennial plants that might be more effective at using deeper soil moisture from rain from the longer intervals, duration of rainfall interval did not affect HR size significantly. We did not directly measure differences in food resources among years, but the abundance of winter rainfall has been shown to affect food supply and subsequently reproduction in *U. inornata* (Mayhew, 1965). Likewise, the effect of rainfall on food supply appears to influence HR size. We propose that using an SPI based on a long-term database rather than on actual monthly or annual totals can better reflect the context of the evolutionary adaptations of the lizard with its environment. The use of SPIs that are based on long-term data sets is especially useful when a species habitat contains a precipitation gradient with few weather stations: the relative magnitude of precipitation events will be similar though the totals may differ. During the period of this study, the region experienced five winters of severe drought (SPI ≤ -1.5; McKee et al., 1993), including two winters with rainfall at two standard deviations (SD) below the mean (Fig. 6). During the nearly 60-yr prior to our study there were no winters with an SPI of ≤ -1.5 SD. Vandergast et al. (2016) examined how drought combined with habitat fragmentation has altered the genetic diversity of this population over time. That the population persists, and we still observe at least some annual reproduction, indicates that localized adaptation to drier conditions may explain some of the genetic divergence found by Vandergast et al. (2016).

Density of adult *U. inornata* has no significant effect on HR size of females but has an inverse relationship that explains about 44% of the variation in the HR size of males. Social factors therefore apparently have an impact on HR size, i.e., the larger HRs of males are determined by availability of females and are structured to increase reproductive success (Andrews, 1971; Schoener and Schoener, 1982; Stamps, 1983; Hews, 1993; Perry and Garland, 2002). However, ecological variables may affect HR size in addition to social factors. For instance, Alberts (1993) reported that HR size of Desert Iguanas (*Dipsosaurus dorsalis*) was not correlated with population density in either sex, possibly because of non-uniform distribution of plants that dictated space use by lizards.

Uma inornata density varied by year, possibly because of rainfall, as it affected food availability that in turn may affect *U. inornata* reproductive output (MF and AM, pers. obs.). However, there was no significant correlation between rainfall and adult density, and that is perhaps because of a lag in plant and animal prey responses to rainfall. The absence of a correlation between lizard density and rainfall allowed us to analyze adult population density independently of rainfall. Because density had a significant inverse relationship with HR size in males, the areas required for mate location might be relatively large in years of low lizard density when compared with years of high lizard density. Our results are consistent with Perry and Garland's (2002) conclusion that the larger HRs of male lizards are determined by availability of females such that reproductive output would be maximized. Castañeda et al. (2007) found that the HR areas of adult male and adult female *U. stejnegeri* were both inversely related to density during the breeding season and that the density of all age classes combined was negatively correlated with HR size during the nonbreeding season of the year. In contrast, Rose (1982) reported that HR sizes of *Uta* and *Sceloporus* were density independent for both sexes.

Additional long-term studies are required in order to fully understand of how different species and populations respond to variations in population density. Clearly long-term studies are more informative than short-term studies because HR size will increase with the age and size of individuals and therefore differ among multiple years. We recommend against combining HR size data for multiple years because it will overestimate space use in any single year. Furthermore, intra- and interspecific HR comparisons should be made among similar age and size class individuals in the analysis. Alternatively, using logistic growth curves as discussed earlier (Table 2) should be explored as an approximation of the average HR size for the largest individuals of a population.

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