

## REPTILE HOME RANGES REVISITED: A CASE STUDY OF SPACE USE OF SONORAN DESERT TORTOISES (*GOPHERUS MORAFKAI*)

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**Abstract.**—Many recommendations exist for estimating home ranges of herpetofauna, often focused on mitigating effects of sedentary behavior and autocorrelation. Authors have often applied minimum convex polygons (MCP) or kernel density estimators (KDE) due to common usage or perceived benefits in comparing studies; however, assumption violations compromise the validity of estimates and comparisons between studies. Recently developed autocorrelated kernel density estimation (AKDE) alleviates these problems, so we applied this methodology to describe space use of Sonoran Desert Tortoises (*Gopherus morafkai*) to identify effects of age and sex on home-range size, fidelity, and range residency, and the effect of environmental condition on space use. We identified several cases of non-range-resident behavior, with immature tortoises more likely to disperse than adults. Home-range estimates from AKDE were less biased than traditional MCP and KDE estimates. Home ranges were highly variable, but range-resident immature females had smaller multi-year home ranges than males and adult females. Annual home ranges did not differ during drought, and male range areas exceeded those of females. The magnitude of annual home-range overlap did not differ by dyad or drought condition, but pairs of gravid females were less likely to overlap than were pairs of non-gravid females, suggesting that study-site productivity and reproduction-related behaviors influence patterns of range overlap. Additional study of the use of permanent rock shelters will illuminate patterns of space use within and between individuals, and long-term study is needed to document survival, settlement, and contribution of dispersing tortoises to new populations, especially relative to anthropogenic habitat fragmentation.

**Key Words.**—autocorrelated kernel density estimation; Brownian bridge; continuous-time movement model; core area; dispersal; minimum convex polygon; overlap; site fidelity; Testudinidae

### INTRODUCTION

Turtles are among the most endangered taxa on earth, and tortoises (Family Testudinidae) are particularly threatened, with those in North America ranging from Near Threatened (Texas Tortoise, *Gopherus berlandieri*) to Vulnerable (Goode's Thornscrub Tortoise, *G. evgoodei*, and Sonoran Desert Tortoise, *G. morafkai*), Endangered (Gopher Tortoise, *G. polyphemus*), and Critically Endangered (Mohave Desert Tortoise, *G. agassizii*, and Bolson Tortoise, *G. flavomarginatus*; Rhodin et al. 2018). In addition to direct threat mitigation (Berry and Aresco 2014), determining factors that affect space use for turtles and tortoises could improve conservation planning by identifying how movement influences demography and population dynamics (Allen and Singh 2016; Slavenko et al. 2016). One important aspect of space use is the home range

of an individual, defined by Burt (1943) as the “area traversed by the individual in its normal activities such as food-gathering, mating, and caring for young.”

The ecological literature is replete with reviews and recommendations concerning home range estimation (e.g., Seaman and Powell 1996; Girard et al. 2002; Laver and Kelly 2008; Fieberg and Börger 2012; Signer et al. 2015). The implications and challenges of dealing with temporal autocorrelation among tracking data when estimating home ranges have attracted considerable attention with conflicting recommendations (e.g., Swihart and Slade 1985; Rooney et al. 1998; Blundell et al. 2001; Fieberg 2007; Kie et al. 2010). In the herpetological literature, recommendations for home-range estimation have been motivated in part by the sedentary behavior of herpetofauna and their use of retreats multiple times during the active season (e.g., Bauder et al. 2015; Silva et al. 2018). For example,

both Row and Blouin-Demers (2006) and Harless et al. (2010) recommended the combined use of minimum convex polygons (MCP) and kernel density estimators (KDE) to estimate home-range size of herpetofauna, with the MCP suggested to represent the total amount of area potentially used by the animal and the kernel estimate identifying specific areas of intensive use (e.g., Mata-Silva et al. 2018; Pascoe et al. 2019). Further justification of calculating MCPs for total space use has included the ability to compare home ranges between studies due to the common application of the method (Kazmaier et al. 2002; Perry and Garland 2002; Rautsaw et al. 2018) despite flaws in MCP estimation that may render such comparisons invalid (Powell 2000; White and Garrott 1990). Börger et al. (2006) went so far to state that MCPs should not be used at all to estimate home range size, and results of studies using MCP should be treated with caution due to considerable and unpredictable biases of the method.

In the broader literature on non-parametric density estimation, KDE is known to be statistically optimal (Silverman 1986). Like MCP, however, kernel-based methods have historically relied on the assumption of independent and identically distributed (IID, Table 1) data, which is usually violated by modern animal tracking data (Noonan et al. 2019). Recently, a family of kernel-density methods have been developed that instead condition on a selected autocorrelation model, dubbed autocorrelated KDE (AKDE; Table 1; Fleming et al. 2015; Fleming and Calabrese 2016; Fleming et al. 2018).

Separate from the issue of how home ranges have historically been estimated, most studies of home ranges of North American *Gopherus* occurred over durations of only 1–2 y and included fewer than 30 individuals per population (Berish and Medica 2014). The primary requirement for understanding animal space use sufficiently enough to contribute to conservation and management, however, is the availability of movement data appropriate to the management objective (e.g., estimation over a time period long enough to make general conclusions on movement patterns; Allen and Singh 2016). In addition, sample sizes must be large enough to make population-level inferences and not be overly influenced by individual idiosyncrasies (Börger et al. 2006). In this paper, we describe the space use and home ranges of 43 individual Sonoran Desert Tortoises (*Gopherus morafkai*) monitored over periods of up to 10 y (> 80% more than 2 y) in a population in central Arizona. One objective was to contrast differences between AKDE, KDE, and MCP estimation from our data set.

Activity patterns of the two sister species of desert tortoises, *G. morafkai* and *G. agassizii*, are driven by precipitation and seasonal vegetation amplitude. In

the Mojave Desert, where rainfall is less predictable, tortoise occurrence was driven by precipitation of the driest month, while occurrence in the Sonoran Desert was best explained by precipitation seasonality (Inman et al. 2019). *Gopherus morafkai* exhibit bi-modal activity patterns related to winter-spring precipitation and late summer monsoons (Averill-Murray et al. 2002a). Female activity begins earlier in the spring for females but is higher for both sexes during late summer as courtship and breeding occur July-September (Averill-Murray et al. 2002a). We aimed to describe tortoise space use over time, discriminating differences in age and sex versus individual effects. The duration and scope of our study allowed us to quantify range residency and fidelity across years, as well as frequency of dispersal or exploratory movements (e.g., occasional sallies of Burt 1943).

We also investigated overlapping space use between tortoises relative to contrasting predictions about degree of drought. For example, *G. agassizii* in two populations had smaller home ranges during a drought year (precipitation 25% of the long-term average) than the previous, productive year (225% precipitation; Duda et al. 1999), suggesting that overlap between individuals should be lower during drought conditions than during more productive years. Alternatively, an inverted U-shaped relationship has been hypothesized between territoriality (i.e., minimum home range overlap) and food resources (Maher and Lott 2000). This model suggests that with low food abundance (e.g., during extreme drought), the cost of defending resources exceeds the energy gained from the resources, resulting in high overlap among home ranges; however, with moderate food abundance (e.g., during typical rainfall conditions), the cost-benefit ratio shifts toward overlap reduction or exclusiveness. Finally, with super-abundant food resources (e.g., resulting from above-average rainfall), there is no economic benefit from territory exclusiveness, so home range overlap increases. This model has been extended to suggest that home ranges should also increase in size as habitat quality decreases (McLoughlin et al. 2000).

## MATERIALS AND METHODS

**Study site.**—We studied *G. morafkai* in the northeastern Sonoran Desert near Sugarloaf Mountain on the Tonto National Forest, Maricopa County, Arizona, USA. The study area occurred within the Paloverde (*Parkinsonia microphylla*)-Mixed Cacti series of the Arizona Upland Subdivision of the Sonoran Desert (Turner and Brown 1982). Arroyos divided a rolling topography of steep, rocky slopes with boulders up to 4-m diameter. Except for dispersing tortoises described later, the study occurred over approximately

**TABLE 1.** Home-range estimators, movement models, and other terms used in analyses of Sonoran Desert Tortoise (*Gopherus morafkai*) space use. See Fleming et al. (2014) and Calabrese et al. (2016) for an overview.

Term	Notation	Meaning
Home-range Estimators and Associated Terms		
Autocorrelated Kernel Density Estimator	AKDE	Kernel-density methods conditioned on a selected autocorrelation model (Fleming et al. 2015; Fleming and Calabrese 2016; Fleming et al. 2018)
Kernel Density Estimator	KDE	Non-parametric estimation of the utilization distribution from a sample of locational observations, assuming IID data (Worton 1989); “conventional” kernel density home-range estimator
Minimum Convex Polygon	MCP	The smallest polygon around points at the specified percentage with all interior angles less than 180 degrees; assumes IID data (Hayne 1949)
Bhattacharyya coefficient	BC	Measure of similarity between two probability distributions, ranging from 0 (no overlap) to 1 (identical distributions); used as a measure of proportional home-range overlap because it does not require an arbitrary quantile to be specified (Winner et al. 2018)
Mahalanobis distance	MD	Measure of the distance between two distributions (Mahalanobis 1936)
Effective sample size	$\hat{N}_{\text{area}}$	In IID data $\hat{N}_{\text{area}}$ equates to the number of observed locations; in autocorrelated data $\hat{N}_{\text{area}}$ is the equivalent amount of IID data to produce the same quality estimates (< number of observed locations)
Movement Models and Associated Terms		
Independent and identically distributed	IID	Random search for resources in a defined area with uncorrelated positions and velocities; leads to conventional kernel density estimation
Brownian motion	BM	Random search in an area of infinite extent with correlated positions, uncorrelated velocities, and no home range
Integrated Ornstein-Uhlenbeck movement	IOU	Random search within a defined area, with both correlated positions (over time scales $\tau_r$ ) and correlated velocities ( $\tau_v$ ) and no home range
Ornstein-Uhlenbeck movement	OU	Random search within a defined area, with correlated positions (over time scales $\tau_r$ ) and uncorrelated velocities
Ornstein-Uhlenbeck-F movement	OUF	Random search in an area of infinite extent with both correlated positions (over time scales $\tau_r$ ) and correlated velocities (over time scales $\tau_v$ )
Position-autocorrelation time scale	$\tau_r$	Time scale associated with the animal covering its home range (home-range crossing time; relevant only to OU and OUF)
Velocity-autocorrelation time scale	$\tau_v$	Time scale over which an animal tends to maintain its present speed and direction; relevant only to OUF and IOU

120 ha, with elevations from 650 m to 768 m. A state highway delineated the eastern boundary of the core study area, and recreational target shooters heavily used the southern-most boundary.

We characterized the annual environmental condition at Sugarloaf with the standardized precipitation-evapotranspiration index (SPEI) provided by the Terrestrial Precipitation Analysis tool (Lemoine et al. 2016). SPEI is a standardized index of precipitation that indicates the amount of water surplus or deficit relative to atmospheric demand (Vicente-Serrano et al. 2010). Negative values of SPEI indicate drought conditions, and positive values indicate non-drought conditions.

**Data collection.**—We used telemetry to monitor 29 female tortoises (184–289 mm midline carapace length [CL]) year-round from 1996 through 2005 as part of a reproductive ecology study (Averill-Murray 2002; Averill-Murray et al. 2018). We attached VHF

radio transmitters (< 5% body weight; AVM Instrument Company, Colfax, California, USA; Telonics, Mesa, Arizona, USA; or Wildlife Materials, Murphysboro, Illinois, USA) to the anterior carapace using 5-minute gel epoxy (Devcon, Illinois Toolworks, Inc., Hartford, Connecticut, USA) and we tracked tortoises weekly. With one exception in 1998, we began adding males (191–265 mm CL) to regular telemetry monitoring in 2001 (n = 9; Supplemental Information: Appendix A).

We excluded observations between the first and last dates of hibernation from movement and home range modeling, estimating the date that each tortoise terminated hibernation (Gregory 1982) as the last day the tortoise was observed inside or < 10 m from its hibernaculum. Monitoring periods of telemetered tortoises spanned 2–10 y, and total number of observations ranged from 24 to 313 per tortoise. We also included opportunistic observations without telemetry, primarily when the cumulative number of

such observations produced sample sizes  $> 10$  for additional male tortoises. Overall, we recorded a mean of 129 total observations per tortoise, with annual means ranging from 29 to 34 (Supplemental Information, Appendix A).

**Movement and home range.**—We calculated variograms, fit movement models, and estimated spatial probability density functions via area-corrected, autocorrelated kernel density estimation (AKDE<sub>c</sub>) that were optimally weighted to determine home ranges using the continuous-time movement model (ctmm) package in R 3.5.0 (Calabrese et al. 2016; Fleming and Calabrese 2016, 2018; R Core Team 2018). For each tortoise, we plotted the estimated semi-variance as a function of time lag to visually inspect the autocorrelation structure of the location data (Fleming et al. 2014; Calabrese et al. 2016). Variograms of individuals exhibiting home-range behavior (i.e., range residents) reveal an asymptote on a timescale that roughly corresponds to the home-range crossing time, while the plotted semi-variance of non-range residents does not approach an asymptote (Fig. 1).

We did not estimate home ranges for non-range residents, although visual inspection of location data allowed us to truncate dispersal or exploratory movements from the primary cluster of observations for some individuals to estimate home ranges during periods of range residency. We confirmed range residency for the non-truncated data with variograms. We used starting values derived from the semi-variance functions to fit movement models (Table 1) via maximum likelihood estimation with model selection based on Akaike Information Criteria adjusted for small sample size (AIC<sub>c</sub>; Fleming et al. 2014; Calabrese et al. 2016). We estimated the mean speed of extracted dispersal or exploratory trajectories using the speed() function in ctmm, which simulates multiple realizations of the trajectory of an individual to estimate the time-averaged speed.

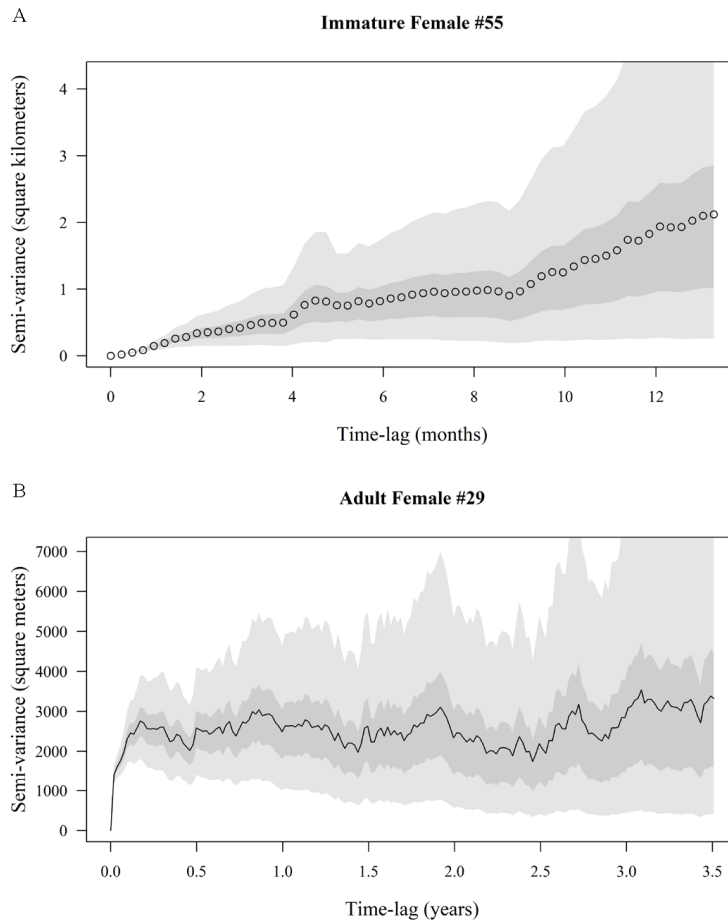
We estimated home ranges using AKDE<sub>c</sub> conditional on the selected model for each tortoise (Fleming et al. 2015; Fleming and Calabrese 2016). We estimated core areas as the area encompassed by the 50% AKDE<sub>c</sub> isopleth, the proportion of the total (95%) home range area contained by the 50% core area (PA), and the intensity of core area use ( $I = PA/0.50$ ; Samuel et al. 1985). We used a bias-corrected Bhattacharyya coefficient (BC; Table 1) to estimate overlap of AKDE<sub>c</sub> home ranges between individuals and to estimate overlap within individuals as a measure of site fidelity across years.

For comparison, we estimated conventional 95% MCP home ranges using the adehabitatHR package in R (Calenge 2006). We also conducted a cross-validation exercise similar to that by Noonan et al. (2019) to

quantify the ability of AKDE<sub>c</sub>, KDE adjusted for small sample size (KDE<sub>c</sub>), and MCP estimates generated from roughly the first half of observations of each individual to include 95% of the second half of the locations of individuals. We divided the data for each tortoise between complete activity seasons to include as close to half the total observations as possible. We conducted cross-validation for the complete set of tortoises, as well as on a reduced set that excluded tortoises with dissimilar movement patterns between periods as indicated by a positive BC (see Noonan et al. 2019). Because performance improved with effective sample size ( $\hat{N}_{\text{area}}$ ; Table 1) in an asymptotic and nonlinear fashion, we used package drc (Ritz et al. 2015) to fit Michaelis-Menten curves ( $f(x) = Lx/(x_0 + x)$ ) to the results via median quantile regression to summarize trends between estimators.

**Hypotheses, predictions, and statistical analyses.**—We sought to better understand the nature of dispersal and potential differences with temporary exploratory movements. Under the hypothesis that immature tortoises have not yet established permanent home ranges, we predicted that (1) immature tortoises were more likely to exhibit non-range-resident behavior than mature tortoises. We further hypothesized that dispersal and temporary explorations would differ in movement characteristics and tested the predictions that (2) movement rate did not differ between dispersal and exploratory movements, and (3) annual path length (i.e., the summed straight-line distance between observation points) did not differ between dispersal and exploratory movements. For our first prediction, we combined males and females due to small sample sizes. We used a size cutoff of 220 mm CL for females and 210 mm CL for males as the minimum sizes of sexual maturity documented from this population (Averill-Murray et al. 2018; Owens et al. 2019).

Next, we examined cumulative home ranges (i.e., across all years or observations for each tortoise) of the range-resident tortoises. We included the single immature, range-resident male with all males to minimize unbalanced sample sizes after preliminary graphical diagnostics suggested minimal differences in AKDE<sub>c</sub> between it and larger males. We hypothesized that tortoises in different sex/age classes use space differently and predicted that sex/age classes (adult females, immature females, and males) differed in (4) AKDE<sub>c</sub> home-range size, (5) home-range crossing time ( $\tau_c$ ; Table 1), (6) core-area size, and (7) intensity of core-area use. For predictions 4–6, we applied mixed-effects, within-study meta-analyses to explicitly account for the variation (heterogeneity) among the true effects arising from estimated uncertainty in home-range size within individual tortoises (Mengerson et al. 2013).



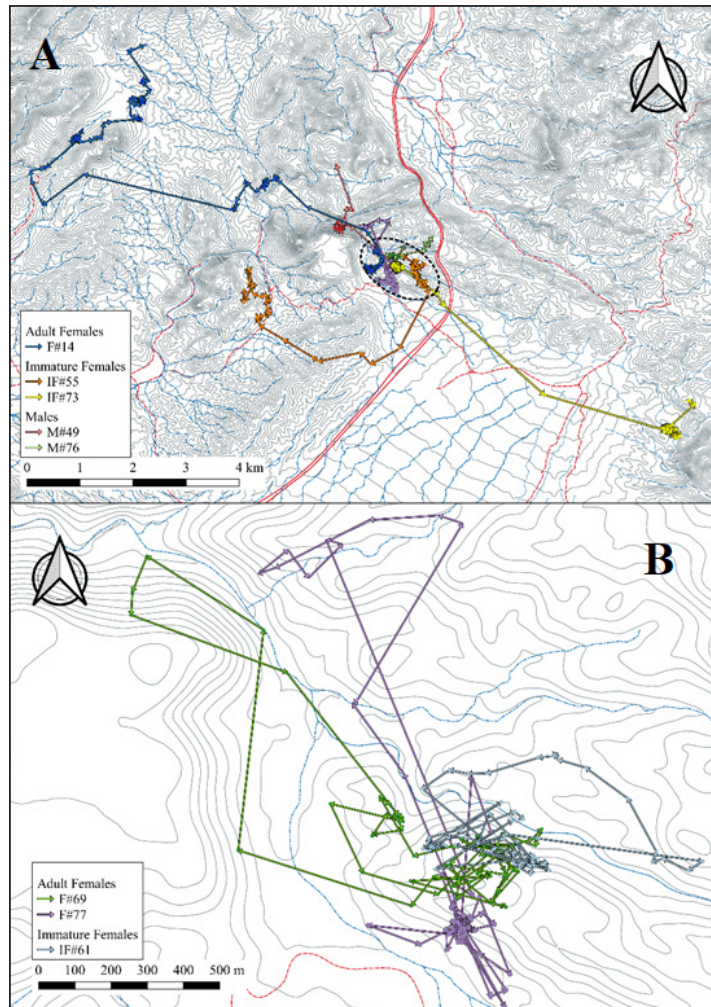
**FIGURE 1.** Variograms illustrating lack of range-resident behavior with no asymptote (A) and an asymptote characteristic of range-resident behavior (B) of Sonoran Desert Tortoises (*Gopherus morafkai*). Dark gray and light gray shading indicates 50% and 95% confidence bands, respectively.

We report  $I^2$ , which estimates how much of the total variability in the effect-size estimates can be attributed to heterogeneity among the true effects, and  $H^2$ , which estimates the ratio of the unaccounted variability in the effect-size estimates to the amount of sampling variability (Higgins and Thompson 2002). Thus, a complete absence of heterogeneity between individual tortoises would produce  $I^2 = 0$  and  $H^2 = 1$ .

We examined annual home ranges beginning with the predictions that (8) AKDE<sub>C</sub> home-range size does not change systematically as data from sequential years are added for each individual, and (9) precision in estimated home-range size increases as data from sequential years are added. Next, we hypothesized that annual space use differs among tortoises in different sex/age classes, including females differing in reproductive activity. We predicted that (10) home-range fidelity differed between adult females, immature females, and males and that fidelity decreased with increasing intervals (2–8 y) between annual estimates. We also predicted that gravid females, non-gravid females, immature females, and

males differed in (11) AKDE<sub>C</sub> home-range size, (12) home-range crossing time ( $\tau_r$ ), (13) core-area size, and (14) intensity of core-area use.

Lastly, we investigated the prediction (15) that gravid females, non-gravid females, immature females, and males did not differ in proportion of home-range overlap among dyads. Home ranges of geographically distant individuals are inherently less likely to overlap than those of more proximal individuals, and including every individual in the analysis could have confounded interpretations of overlap patterns. The probability that any two home ranges overlap is contingent on how neighboring individuals with potentially overlapping home ranges are defined. Therefore, we used the Mahalanobis distance (MD; Table 1) between home-range pairs as a covariate to adjust for (dis-)similarity between the paired distributions, excluding pairs of immature females from the analysis due to much smaller sample size. The largest MD between overlapping home ranges was 6.68, so we excluded all dyads with larger MDs from the analyses. We re-set overlap values to zero



**FIGURE 2.** Movement paths of Sonoran Desert Tortoises (*Gopherus morafkai*) that dispersed from the core study area (A) or made temporary, exploratory movements (B) at Sugarloaf Mountain, Arizona. Black, dashed ellipse: core study area; solid red lines: divided state highway; dashed red lines: unpaved roads; dashed blue lines: dry stream beds. Topographic contour interval = 12.2 m.

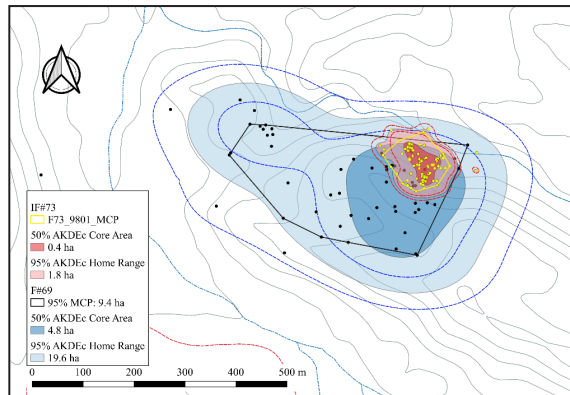
if confidence limits indicated a lack of support of actual overlap (i.e., BC lower 95% confidence limit < 0.01; Winner et al. 2018). We chose not to look separately at patterns in the number of individuals overlapping the home range of each tortoise (e.g., Harless et al. 2009) due to the confounding effects of defining neighboring tortoises and the limit of potential neighbors of tortoises on the periphery of the study site.

Additional details on model structure and software packages used for each prediction are provided in Appendix B of the Supplemental Information. We evaluated model assumptions (e.g., normality, homoscedasticity) by visual examination of residual plots, Q-Q plots, likelihood profile plots, worm plots, and detrended transformed Owen's plots in metafor, gamlss, and MuMIn (Bartoń 2014), as applicable. For inference, we relied on full models after eliminating non-significant interaction terms ( $\alpha = 0.05$ ; Fieberg and

Johnson 2015; Dormann et al. 2018). We conducted contrasts between marginal means with multcomp (Hothorn et al. 2008) or emmeans (Lenth 2019). For zero- or one-inflated analyses in gamlss, we followed model-selection procedures described by Stasinopoulos et al. (2017). We report contrasts on the link scale and parameter estimates on the response scale with 95% confidence intervals in reference to statistical clarity (Dushoff et al. 2018).

## RESULTS

**Dispersal and occasional sallies.**—Visual inspection of variograms (e.g., Fig. 1A; Supplemental Information, Appendix C) and location data identified five tortoises that dispersed from the core study area (Fig. 2A): adult female #14 (249 mm CL, maximum displacement = 7.0 km), immature females #55 (208 mm, 3.6 km) and



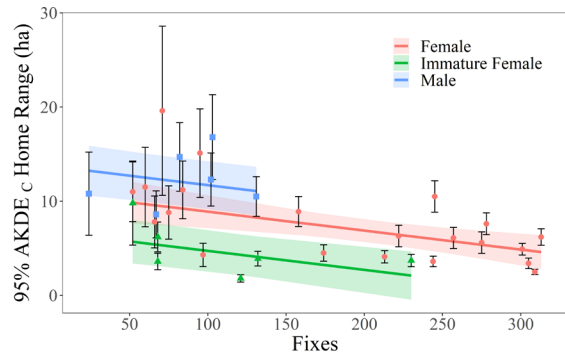
**FIGURE 3.** Representative 95% minimum convex polygons (MCP), 95% area-corrected, optimally weighted autocorrelated kernel density estimate (AKDE<sub>c</sub>) home ranges, and 50% AKDE<sub>c</sub> core areas for two Sonoran Desert Tortoises (*Gopherus morafkai*) at Sugarloaf Mountain, Arizona. AKDE<sub>c</sub> 95% confidence bands are shown with dashed lines.

#73 (173 mm, 6.7 km), and immature males #49 (200 mm, 2.6 km) and #76 (191 mm, 1.0 km). In addition, three tortoises made temporary exploratory movements (sallies) lasting 5–26 weeks (Fig. 2B): adult females #69 (maximum 1.4 km from last observation in normal range), #77 (1.3 km), and immature female #61 (0.5 km). Overall, immature tortoises were 54% more likely on average to exhibit non-range-resident behavior than larger, older tortoises (Supplemental Information, Appendix B.1). This trend was similar when excluding temporary sallies, with immature tortoises 47% (95% CI = 18–76%) more likely to disperse than mature tortoises.

Male #76's dispersal occurred in the final two months prior to its transmitter being removed, and the tortoise exhibited range residency during its initial 24 observations over approximately 1 y. Dispersal of four tortoises spanned two or more activity seasons (Table 2). Female #14 and immature female #73 exhibited range residency within one or more years under study, and we include these ranges in the relevant analyses below. Immature female #61 made an extended sally that spanned winter hibernation before she returned to her previous home range.

Annual path length ranged from 0.9 km to 7.3 km ( $\bar{x} = 3.3 \pm$  [standard deviation] 2.17 km) for dispersal movements and from 0.7 km to 3.7 km ( $\bar{x} = 2.1 \pm 1.41$  km) for sallies (Table 2). Dispersers moved an estimated 21–177 m/d ( $\bar{x} = 59.8 \pm 49.00$  m/d), and sallies involved moving an estimated 20–85 m/d ( $\bar{x} = 46.0 \pm 29.70$  m/d; Table 2). Differences between dispersal and sallies are statistically unclear based on contrast CIs overlapping zero for both path length and rate of movement (Supplemental Information, Appendix B.2–3).

**Cumulative home ranges.**—Excluding temporary sallies allowed us to fit a range-resident model and



**FIGURE 4.** Predicted cumulative 95% optimally weighted autocorrelated kernel density estimate (AKDE<sub>c</sub>) home ranges (with associated 95% confidence intervals) against number of fixes (back-transformed from the standardized variable) for Sonoran Desert Tortoises (*Gopherus morafkai*) at Sugarloaf Mountain, Arizona. Bands indicate the 95% confidence region for the relationship.

estimate a home range for those individuals. We determined 22 adult females, five immature females (including immature #73 for > 3 y before and after her dispersal event), and 13 males to be range resident during the study. Variograms included asymptotic semi-variance (e.g., Fig. 1B), although those from individuals with < 122 records were often sparser or erratic, especially if derived from opportunistic observations across several years (e.g., Male #318 in Supplemental Information, Appendix C). In all but seven cases, an OU process was selected as the best movement model (83%), with IID movement (17%) selected in the remaining instances (Supplemental Information, Appendix D). Only one of the IID cases (adult female #68) involved a tortoise monitored over multiple complete seasons and with > 100 observations ( $\hat{N}_{\text{area}} > 23$ ); the other six cases involved tortoises with fewer than 24 observations spread over 2–7 y.

Ninety-five percent AKDE<sub>c</sub> home ranges varied from 1.8 to 19.6 ha among adult females ( $\bar{x} = 7.8 \pm 4.14$  ha), immature females ( $4.8 \pm 2.81$  ha), adult males ( $10.6 \pm 4.54$  ha), and immature males (10.8 ha,  $n = 1$ ; Fig. 3; Supplemental Information, Appendices D–E). Analysis of AKDE<sub>c</sub> home range as a function of tortoise sex/age and number of fixes revealed considerable heterogeneity among tortoises ( $I^2 = 96.6\%$ ,  $H^2 = 29.0$ ). Immature females had smaller home ranges than adult females and males, but we did not find a statistically clear difference between males and adult females (Supplemental Information, Appendix B.4). Home-range size decreased with more fixes (Fig. 4).

With one exception, 95% MCP home ranges consistently underestimated AKDE<sub>c</sub> estimates, with the magnitude of difference shrinking with  $\hat{N}_{\text{area}}$  (Fig. 5; Supplemental Information, Appendices D–E). Fifteen of 41 individuals (37%) for which there were sufficient

**TABLE 2.** Dispersal and temporary sallies for Sonoran Desert Tortoises (*Gopherus morafkai*) at Sugarloaf Mountain, Arizona. Ninety-five percent confidence intervals of mean speed are given in parentheses. The abbreviation SD = standard deviation.

Sex/ID	Start Date	End Date	Duration (d)	# Observations	Mean Speed (m/d)	Net Displacement (m)	Path Length (m)
<b>Dispersal</b>							
F#14	1 July 1998	4 Nov 1998	126	18	36 (31–41)	2831	3824
	30 April 1999	16 Sept 1999	139	19	72 (57–88)	3611	7320
	29 March 2001	19 Oct 2001	204	28	29 (20–38)	1503	3218
	3 July 2002	8 Nov 2002	128	13	21 (16–27)	1248	1977
iF#55	11 Sept 1997	26 Nov 1997	76	11	91 (73–111)	3279	4991
	17 April 1998	1 Oct 1998	167	24	29 (20–38)	390	3118
iF#73	10 Aug 2001	2 Nov 2001	84	7	177 (106–256)	6174	6498
	6 Aug 2004	29 Sept 2004	54	4	31 (17–47)	749	904
iM#49	23 Aug 1996	1 Oct 1996	39	6	87 (50–129)	1318	1857
	10 April 1997	8 May 1997	28	5		1547	1807
iM#76	1 July 1998	11 Sept 1998	72	11	25 (14–38)	780	907
Mean (SD)			101.5 55.58	13.3 8.03	59.8 49.00	2130.0 1711.33	3311.0 2170.00
	<b>Sallies</b>						
iF#61	1 Oct 1996	30 Dec 1996	90	13	26 (14–41)	286	1174
	6 March 1997	24 April 1997	49	8	20 (13–28)	353	685
F#69	13 Aug 1999	2 Oct 1999	50	9	85 (42–135)	279	2906
F#77	11 June 1998	11 Sept 1998	92	15	53 (39–68)	50	3658
Mean (SD)			70.3 23.98	11.3 3.30	46.0 29.70	242.0 132.27	2105.8 1406.72

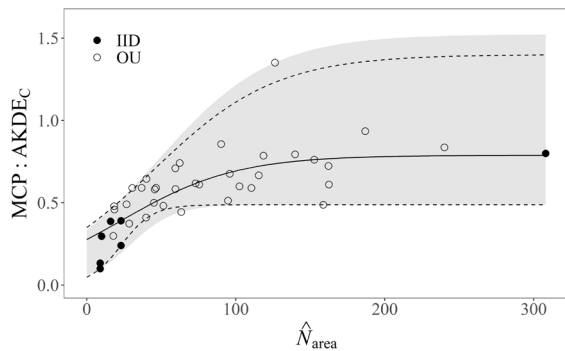
data to divide for cross-validation had dissimilar ranges between the two periods ( $BC = 0.04\text{--}0.63$ ). Inspection of range plots estimated from each period confirmed that these differences resulted from slight expansion from, or constriction of, the first-period range in every case rather than marked distributional shifts. We found that 95% AKDE<sub>c</sub> home ranges from the first half of locations of each individual included closer to the nominal proportion of the second-half locations in every case compared to MCP estimates (e.g., Fig. 6); KDE<sub>c</sub> estimates included more locations than AKDE<sub>c</sub> in only a single instance (by 1%). Compared to the nominal 95% quantile, AKDE<sub>c</sub> and KDE<sub>c</sub> estimates included a median 95% and 93% of second-half locations, respectively, whether the ranges were dissimilar between periods, compared to 70–72% for MCP. The 95% confidence band broadly covered the nominal level for AKDE<sub>c</sub>, slightly less so at small  $\hat{N}_{\text{area}}$  for KDE<sub>c</sub>, and not at all for MCP except marginally at the highest  $\hat{N}_{\text{area}}$  (Fig. 7).

Home-range crossing time ( $\tau_r$ ) varied from 2 to 29 d among adult females ( $\bar{x} = 12.3 \pm 5.83$  d), immature females ( $10.0 \pm 5.97$  d), and adult males ( $8.4 \pm 3.26$  d; Supplemental Information, Appendix D). We found no statistically clear differences in  $\tau_r$  between sexes and no

clear relationship to the number of fixes (Supplemental Information, Appendix B.5). There was substantial heterogeneity in  $\tau_r$  among tortoises ( $I^2 = 83.3\%$ ,  $H^2 = 5.6$ ).

Fifty percent AKDE<sub>c</sub> core areas varied from 0.3 to 4.8 ha among adult females ( $\bar{x} = 1.7 \pm 1.13$  ha), immature females ( $0.9 \pm 0.76$  ha), adult males ( $2.2 \pm 0.79$  ha), and immature males (2.4 ha,  $n = 1$ ; Fig. 3; Supplemental Information, Appendices D–E). As with 95% AKDE<sub>c</sub>, immature females had smaller core areas than adult females and males, and we did not find a statistically clear difference between males and adult females (Supplemental Information, Appendix B.6). Core-area size also decreased with more fixes (Fig. 8). The model also revealed considerable heterogeneity among tortoises ( $I^2 = 97.6\%$ ,  $H^2 = 41.8$ ). We found no clear relationship between core areas as proportions of the total home range and AKDE<sub>c</sub> home-range size ( $r = 0.18$ ,  $CI = -0.14\text{--}0.46$ ). Relative intensity of use of core areas ranged from 1.69 to 4.16 ( $\bar{x} = 2.51 \pm 0.588$ ; Supplemental Information, Appendix D), but we found no clear relationship to sex/age (Supplemental Information, Appendix B.7).





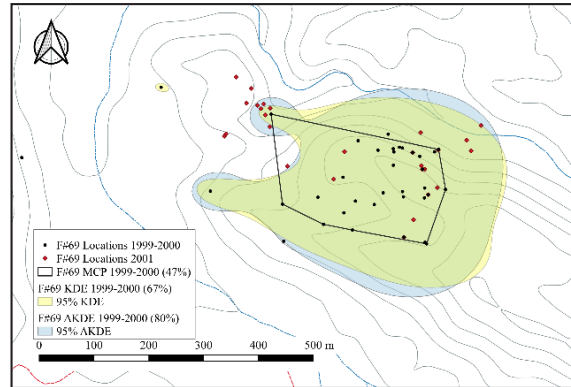
**FIGURE 5.** Ratio of 95% minimum convex polygon (MCP) home range estimates to 95% optimally weighted autocorrelated kernel density estimate (AKDE<sub>c</sub>) estimates as a function of effective sample size ( $\hat{N}_{\text{area}}$ ) for Sonoran Desert Tortoises (*Gopherus morafkai*) at Sugarloaf Mountain, Arizona. The solid line represents the fit of a logistic curve to the data. Dashed lines and the gray band encompass 90% and 95% confidence bands, respectively. Acronyms IID = independent, identically distributed model and OU = Ornstein-Uhlenbeck model.

**Annual environment and home ranges.**—Total annual precipitation ranged from 150 mm in 2002 to 554 mm in 1998. Correspondingly, SPEI ranged from -8.34 to 6.30. Drought conditions occurred during half the years of the study (Table 3).

Of 140 individual/year combinations, an OU process was selected as the best movement model 114 times (81%), IID 25 times (18%), and OUF once (0.7%; Supplemental Information, Appendix F). We found no clear effect on home-range size by increasing  $\hat{N}_{\text{area}}$  as additional years were added for each tortoise, although the width of the 95% CI decreased quadratically with  $\hat{N}_{\text{area}}$  (Supplemental Information, Appendix B.8–9; Fig. 9). Likewise, we found no clear trend in home-range size over time. Rather, tortoises showed strong fidelity among their annual home ranges (overall  $\bar{x} = 0.83 \pm 0.123$ ). We found no evidence of an effect of sex/age class or interval between years on mean home-range fidelity (Supplemental Information, Appendix B.10).

Annual 95% AKDE<sub>c</sub> home-range areas ranged from 0.5 to 24.2 ha (Supplemental Information, Appendix F). As with cumulative AKDE<sub>c</sub> home ranges, considerable heterogeneity existed between individuals in annual home ranges ( $I^2 = 93.7\%$ , between-individual heterogeneity = 69.1%, within-individual heterogeneity = 24.6%). Males had larger home ranges than gravid females, non-gravid females, and immature females, but we did not find statistically clear differences between female comparisons (Fig. 10). We also found no clear relationship between annual home-range size and SPEI (Supplemental Information, Appendix B.11).

Home-range crossing time ( $\tau_r$ ) varied from 2 to 48 d (Supplemental Information, Appendix F). We found no statistically clear differences in  $\tau_r$  between sex/age classes and no clear relationship to SPEI (Supplemental



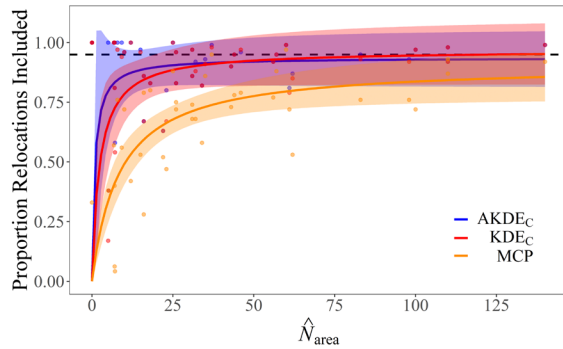
**FIGURE 6.** Example cross-validation results for Female Sonoran Desert Tortoise (*Gopherus morafkai*) #69. Home-range polygons were derived from observations in 1999–2000 ( $n = 41$ ) with 95% minimum convex polygon (MCP); 95% area-corrected, kernel density estimate (KDE); and 95% area-corrected, optimally weighted autocorrelated kernel density estimate (AKDE). Percentages in the legend are the proportions of observations in 2001 ( $n = 30$ ) contained in the 1999–2000 home-range estimates. AKDE better predicted future space use than did MCP or KDE.

Information, Appendix B.12). There was moderate heterogeneity in  $\tau_r$  between tortoises ( $I^2 = 40.1\%$ , between-individual heterogeneity = 15.4%, within-individual heterogeneity = 24.7%).

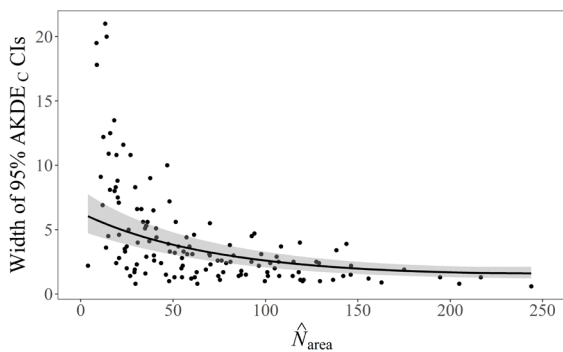
Annual core areas ranged from 0.1 to 6.4 ha (Supplemental Information, Appendix F). As with annual 95% AKDE<sub>c</sub>, males had larger core areas than gravid females, non-gravid females, and immature females, and we did not find statistically clear differences between female comparisons (Fig. 10). We also found no clear relationship between annual core-area size and SPEI (Supplemental Information, Appendix B.13). Considerable heterogeneity existed among individuals in annual core areas ( $I^2 = 96.0\%$ , among-individual heterogeneity = 70.4%, within-individual heterogeneity = 25.4%).

We found no clear relationship between annual core areas as proportions of the home range and annual home-range size in six of eight years ( $|r| = 0.00$ – $0.45$ , all 95% CIs overlap zero), while they were moderately positively correlated in 1998 ( $r = 0.57$ , CI = 0.18–0.81) and 2002 ( $r = 0.50$ , CI = 0.05–0.79). Relative intensity of use of annual core areas ranged from 1.64 to 4.05 (overall  $\bar{x} = 2.29 \pm 0.483$ ; Supplemental Information, Appendix F), but we found no clear relationship to sex/age or drought condition (Supplemental Information, Appendix B.14).

As many as nine tortoises overlapped the annual home range of an individual tortoise, and annual home-range overlap ranged up to 0.99 (Supplemental Information, Appendix G). After controlling for the decreasing effect of MD on mean overlap, we found no clear evidence that mean overlap was affected by sex/age combination or SPEI. Pairs of gravid females were less likely to overlap



**FIGURE 7.** Plots of the percentage of locations from the second half of data included in 95% home ranges estimated from the first half of data as a function of effective sample size ( $\hat{N}_{\text{area}}$ ) for Sonoran Desert Tortoises (*Gopherus morafkai*) at Sugarloaf Mountain, Arizona. Solid lines represent Michaelis-Menten curves ( $f(x) = Lx/(x_0 + x)$ ) fit to cross-validation results via median quantile regression, with shaded 95% confidence bands. The dashed line represents the nominal 95% quantile at which the estimates should cross-validate. Acronyms  $\text{AKDE}_C$  = optimally weighted autocorrelated kernel density estimate;  $\text{KDE}_C$  = kernel density estimate adjusted for small sample sizes; MCP = minimum convex polygon.

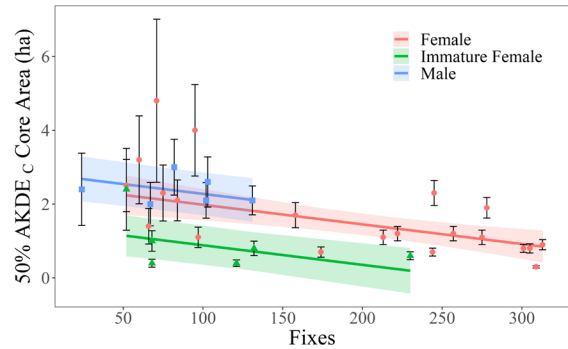


**FIGURE 9.** Width of 95% optimally weighted autocorrelated kernel density estimate ( $\text{AKDE}_C$ ) home range confidence intervals plotted against effective sample size ( $\hat{N}_{\text{area}}$ ) for Sonoran Desert Tortoises (*Gopherus morafkai*). Home range of each tortoise was repeatedly calculated by adding data from each subsequent year of tracking.

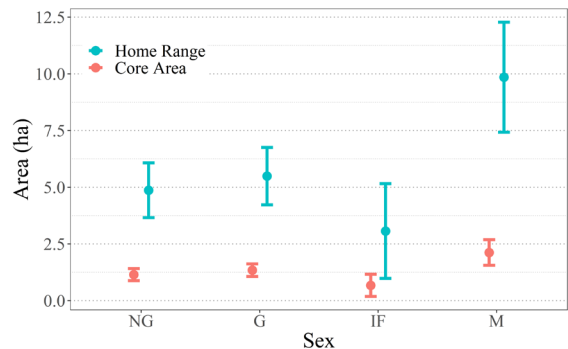
each other than were pairs of non-gravid females at larger MD (Supplemental Information, Appendix B.15; Fig. 11).

### DISCUSSION

**Home range estimation.**—Home-range estimators apply the definition of home range of Burt (1943) by estimating space use while assuming that the focal movement process continues into the future. Under this definition, the home-range area corresponds to the probability distribution of an animal for all realizations of the underlying movement process, thereby representing its range distribution. That is, home-range estimators should extrapolate future space use based on the



**FIGURE 8.** Predicted cumulative 50% optimally weighted autocorrelated kernel density estimate ( $\text{AKDE}_C$ ) core areas (with associated 95% confidence intervals) against number of fixes (back-transformed from the standardized variable) for Sonoran Desert Tortoises (*Gopherus morafkai*) at Sugarloaf Mountain, Arizona. Bands indicate the 95% confidence region for the relationship.



**FIGURE 10.** Predicted annual 95% optimally weighted autocorrelated kernel density estimate ( $\text{AKDE}_C$ ) home-range and 50%  $\text{AKDE}_C$  core-area estimates, with 95% confidence intervals, for each sex/age class of Sonoran Desert Tortoises (*Gopherus morafkai*). Acronyms NG = non-gravid female, G = gravid female, IF = immature female, M = male.

underlying movement process, addressing the question of how much space does an animal need (Fleming et al. 2016). Note that this is a fundamentally different question than asking where was the animal located during the observation period. Brownian bridges (Horne et al. 2007; Kranstauber et al. 2012) address this question by estimating the probability distribution of an animal during the observed timespan (i.e., the occurrence distribution). Areas estimated by Brownian bridges are not estimates of the home-range of an animal but rather a reflection of uncertainty of where it was located while it was being tracked (Fleming et al. 2016, 2017). Nevertheless, Brownian bridges increasingly have been misapplied to estimate home-range areas (e.g., Lei et al. 2017; Thums et al. 2017; Butterfield et al. 2018; Silva et al. 2018; Wolfe et al. 2018), rather than more appropriate applications of occurrence distributions to estimate resource use or to correlate

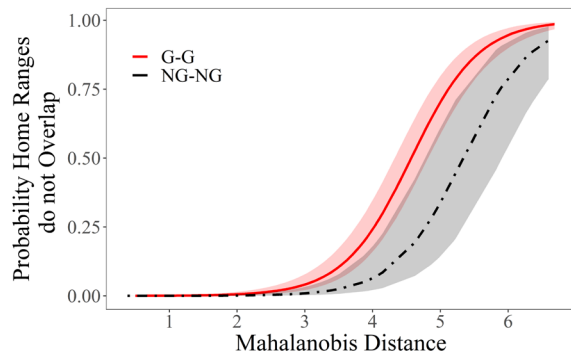
**TABLE 3.** Standardized Precipitation-Evapotranspiration Index (SPEI) and total annual precipitation (mean with standard deviation [SD], in mm) at Sugarloaf Mountain, Arizona, USA, provided by the Terrestrial Precipitation Analysis tool (Lemoine et al. 2016). Negative values of SPEI indicate drought conditions.

Year	SPEI	Annual Precipitation
1996	-4.31	252
1997	-1.05	306
1998	6.30	554
1999	-2.90	305
2000	-2.56	354
2001	1.46	392
2002	-8.34	150
2003	1.24	406
2004	2.58	430
2005	0.31	434
Mean (SD)	-0.73 (4.070)	358 (111.8)
Mean (SD; 1901–2005)	0.29 (3.891)	382 (123.8)

space use with environmental variables (e.g., Marzluff et al. 2004; Byrne et al. 2014; Wells et al. 2014; Vergara et al. 2016).

Autocorrelation is a fundamental issue in applying the definition of home range by Burt (1943) because all home-range estimators currently in widespread use assume statistical independence among observations (Noonan et al. 2019). Past studies simulating coarsely sampled tracking data (e.g., > one day) are often cited as justification for ignoring autocorrelation (De Solla et al. 1999; Blundell et al. 2001; Fieberg 2007). The effects of autocorrelation causing negatively biased MCP estimates in a study of *G. agassizii*, however, led to a recommendation that home ranges be interpreted with caution, downplaying biological interpretation of area as a resource or characteristic of the animal (O'Connor et al. 1994).

Nevertheless, misperceptions that MCP or other estimates that tightly conform to tracking data are more accurate (e.g., Row and Blouin-Demers 2006; Silva et al. 2018) have conditioned ecologists to rely on severely biased methods in trying to answer the question posed above and to apply the results to comparisons with other studies (Noonan et al. 2019). This bias was evidenced by the poor performance of all commonly used home-range estimators to predict future space use in an empirical cross-validation of 369 tracked individuals, although the 22 species in the study included only one reptile (Noonan et al. 2019). Conventional methods generally were found to underestimate the home-range area. Cross-validation of MCP, KDE<sub>c</sub>, and AKDE<sub>c</sub> in our study provided support that this pattern applies more generally among reptiles (Fig. 7). In both studies, the



**FIGURE 11.** The probability that home ranges between pairs of gravid (G) tortoises and pairs of non-gravid (NG) Sonoran Desert Tortoises (*Gopherus morafkai*) do not overlap at Sugarloaf Mountain, Arizona, plotted against Mahalanobis Distance.

difference in accuracy between AKDE and conventional estimators was largest at small effective sample sizes ( $\hat{N}_{\text{area}}$ ). While in IID data  $\hat{N}_{\text{area}}$  equates to the number of observed locations, in autocorrelated tracking data  $\hat{N}_{\text{area}}$  is limited by the number of observed range crossings (Fleming and Calabrese 2016).

Weekly sampling in our study resulted in fewer than 10% IID data sets. Similarly, a 7–10-d tracking interval produced autocorrelated MCP estimates in another study of *G. agassizii* (Franks et al. 2011). Our study resulted in more than 80% of our individual tracking data sets exhibiting autocorrelation in position (OU). Only one case also included autocorrelation in velocity (OUF), but a more frequent sampling schedule (e.g., multiple locations per week or day such as that with increasingly used GPS telemetry) almost certainly would have led to autocorrelation in both quantities because autocorrelation in velocity decays more rapidly than in position (Fleming et al. 2017).

Kazmaier et al. (2002) cautioned against comparison of KDE estimates between studies due to effects caused by differences in sample sizes and smoothing parameters. Later, Harless et al. (2010) addressed limitations of KDE and MCP estimation of *G. agassizii* home ranges, as well as uncritical comparison of home ranges without attention to differences in sampling methodologies between studies, via a comparison of different sampling regimes. They recommended using a particular standardized sampling regime for desert tortoises but still using both home-range estimators, MCP for estimates of the total amount of area potentially used by the animal and KDE for specific areas of intensive use. As Noonan et al. (2019) and we have shown, though, these estimators fail for both purposes. In addition, standardized sampling regimes often will not work because bias in MCP and KDE home-range areas is correlated with  $\hat{N}_{\text{area}}$ , which may not be the same among individuals even under the same sampling regime (Fleming and Calabrese 2016;

Noonan et al. 2019). Finally, for autocorrelated data, increasing sampling frequency results in increasingly negatively biased MCP and KDE estimates, thereby counterintuitively decreasing the accuracy of the home-range estimate by adding more locations (Noonan et al. 2019).

The AKDE family of estimators implemented in *ctmm* accounts for a number of data-quality issues common to animal tracking data, including autocorrelation (Fleming et al. 2015), small effective-sample-size biases (Fleming and Calabrese 2016; Fleming et al., 2019), irregular sampling (Fleming et al. 2018), and telemetry error. Importantly, when tracking data are not autocorrelated, AKDE reduces to KDE, so users do not have to choose between different estimators. In this study, the benefits of AKDE were primarily in its ability to account for autocorrelation and the small effective-sample-size correction, which debiases the area estimates of both KDE and AKDE. Despite not finding a clear trend in estimated home-range size as we sequentially added subsequent years of data for each tortoise, however, our observed trend of decreasing cumulative home-range size with number of fixes runs counter to the small effective-sample-size biases of maximum likelihood estimation and  $AKDE_c$  (Noonan et al. 2019). This is likely an artifact of desert tortoises repeatedly using the same shelters, a common behavior of herpetofauna (Averill-Murray et al. 2002b; Row and Blouin-Demers 2006; Bauder et al. 2015; Sullivan et al. 2016). As an extreme example, between 1997 and 2005, female #68 was found in one particular burrow 146 of 308 observations (47%), not including hibernation. At small  $\hat{N}_{area}$ , this can lead to a positive bias in home-range estimates analogous to spillover bias across (semi-) permeable boundaries (compare to Noonan et al. 2019). Analysis of the data excluding observations in burrows (32–82% of observations) suggested a reduced effect of the number of fixes on home-range size ( $\hat{\beta}_{z,Fixes} = -1.78$ , CI = -3.63–0.07). We expect that more frequent (e.g., with the use of GPS tags) or longer-duration sampling would increase the number of observations outside of burrows and across the full activity and foraging range of each individual, reducing bias at small  $\hat{N}_{area}$ , while use of  $AKDE_c$  would accommodate any increase in autocorrelation among locations.

Importantly,  $AKDE_c$  estimates also include measures of uncertainty not available for the more commonly used MCP. These estimates become more precise with increasing  $\hat{N}_{area}$ , with the wider confidence intervals at low  $\hat{N}_{area}$  tending to compensate for any positive bias due to repeated shelter use. For some species, the ability to account for telemetry error may be of more importance, and *ctmm* features capabilities for both heteroskedastic (circular) GPS errors and (elliptical) VHF errors. Overall, our study reinforces the conclusions of Noonan

et al. (2019) in the superiority of the AKDE family of home-range estimators as specifically applied to the relatively sedentary behavior of many reptiles. Herein, we avoid comparing absolute home-range estimates for *G. morafkai* with those reported for other populations or species given the unknown bias of estimates in the literature. We focus instead on patterns reported from home-range studies in hope that those patterns are less affected by bias than the estimates themselves.

**Occasional sallies and dispersal.**—Consistent patterns of dispersal have yet to emerge from studies of North American tortoises (Guyer et al. 2014). Much of this is due to small samples in most previous studies of home range and to challenges in tracking juveniles or subadults in such studies. Additionally, long-range movements tend to have been discarded with little interpretation because they are difficult to explain and complex to operationally define (Harless et al. 2010). The sample sizes, tracking duration, and application of *ctmm* and the workflow recommended by Fleming and Calabrese (2016) to analyze space use in our study allowed us to largely overcome these challenges. Regarding the *ctmm* workflow, examination of scatterplots and variograms clearly identified non-range-resident, dispersing individuals.

Only one of 35 (3%) telemetered adult tortoises dispersed during the study, while four of eight (50%) immature tortoises exhibited dispersal behavior. In addition, two of 35 (6%) adult tortoises and one of eight immatures (12%) undertook a temporary sally, returning to their established home ranges. Unfortunately, short-term observations appear insufficient to distinguish between dispersal and occasional sallies, as we found the patterns of movement (speed, path length) to be similar between the two behaviors. More frequent observations collected with GPS telemetry may produce data capable of distinguishing between these two behaviors.

Two of nine adult *G. agassizii* monitored in 1 y and five of 10 monitored for 4 y made temporary movements that were > 1 km outside the normal MCP of the animal for one to two weeks (Duda et al. 1999; Freilich et al. 2000). Fifteen of 54 (28%) *G. agassizii* associated with a study investigating the effects of a newly installed barrier fence along a state highway made long-distance movements of 0.8–15.5 km during 2 y of monitoring (Sazaki et al. 1995). While several of the movements in the latter study appeared to be affected by the fence (e.g., linear movements parallel and near the fence), suggested reasons for natural forays or occasional sallies include denning, mating, and use of locally available resources such as mineral deposits (Berry 1986). Although included in overall MCP calculation, several female *G. morafkai* in another population made so-called migratory movements to north slopes

following summer rains, apparently to access higher diversity and abundance of food plants (Sullivan et al. 2016). Previously at Sugarloaf, in June 1992, a female *G. morafkai* (#17) moved approximately 750 m from her previous activity area to a presumed nest site (Averill-Murray et al. 2002a). In 1998, she made a similar movement to a different nesting location approximately 300 m toward that from 1992, although inspection of her variogram and mapped locations indicated that the 1998 movement was less anomalous relative to her other locations that year. For comparison, the longest extent of the entire home range of #17 estimated during this study was approximately 600 m. Similarly, Female #86 moved approximately 400 m north of her presumed normal activity area every summer from 2001 through 2004. Female #86 nested during the period of these movements in 2001, 2002, and 2004 (early July each year), although she also returned to the same area in September 2001 and 2003 while non-gravid. A consistent motivation for these temporary, long-distance movements of *Gopherus* remains unknown and simply may reflect individual idiosyncracies.

Instances of long-distance movement suggestive of dispersal have been reported for adults of several species of *Gopherus* (e.g., Aguirre et al. 1984; Berry 1986; Eubanks et al. 2002), including an exceptional movement of an adult female *G. morafkai* of approximately 32 km (Edwards et al. 2004b). Despite scattered observations of long-distance adult movements, dispersal in reptiles is more often recognized as movement of juvenile or immature individuals away from their natal group (Pough et al. 2004). Male-biased juvenile dispersal (e.g., Kazmaier et al. 2002) is predicted for polygynous reptiles as a result of resource competition, local mate competition, or inbreeding avoidance (Chapple and Keogh 2005). In particular for long-lived individuals where patches of habitat may be occupied for years or decades, adult aggression may stimulate juveniles to disperse (McRae et al. 1981; Tucker et al. 1998). In contrast, we observed only one instance of aggression during the 10-y study (between two adult males on 13 September 1996), and the longest dispersals were made by females.

**Home ranges and core areas.**—High intraspecific variability in home-range area is common among and within turtle populations (Berish and Medica 2014; Slavenko et al. 2016). This also was true at Sugarloaf, with both annual and cumulative home ranges of *G. morafkai* varying over an order of magnitude (0.3–4.8 ha and 1.8–19.6 ha, respectively) and  $I^2 > 96\%$ . Nevertheless, several patterns emerged from the variation. Annual male home ranges and core areas were greater than those of females, irrespective of female age class or reproductive status, consistent

with most short-term studies of *Gopherus* spp. in the literature (e.g., Kazmaier et al. 2002; Franks et al. 2011; Castellón et al. 2018; but see Barrett 1990; Sullivan et al. 2016). Berish and Medica (2014) list several studies that report some immature tortoises with larger home ranges than some adults, but it is not clear whether these estimates reflect range-resident behavior or dispersal movements. Cumulative home ranges and core areas of male and female *G. morafkai* that we estimated over 2–10 y at Sugarloaf were not statistically different, however, suggesting that space use between the sexes may equilibrate over longer than annual time periods. Adult tortoises still had larger ranges than range-resident, immature females over these time periods.

Core areas of *G. morafkai* at Sugarloaf generally were not correlated with home-range size, which is meaningful because animals with home ranges of equal size, but different patterns of home-range use, should have differently sized core areas (Powell 2000). Core areas defined by the 50% AKDE<sub>C</sub> isopleth occupied 12–30% of the total home range, and intensity of core area use was up to 4.2 times the rest of the home range. In comparison, mean core areas of *G. agassizii* (50% MCP) occupied 9–14% of their home ranges (100% MCP), with core areas positively associated with the number of burrows used (Harless et al. 2009). Given the importance of burrows to *G. morafkai*, which are often associated with relatively permanent rock structures (Averill-Murray et al. 2014), burrow usage also likely affects core-area size and intensity of use.

Permanent habitat features such as rock shelters also may anchor *G. morafkai* to their home ranges over time, although patterns of burrow use require additional examination. Range-resident tortoises at Sugarloaf exhibited strong site fidelity, with home ranges overlapping by about 84% across up to 9 y within individuals. In fact, *G. morafkai* may use portions of their home ranges for over a decade (Martin 1995). Mean common-area usage over 2 y was comparable for another population of *G. morafkai* (78–84%; Sullivan et al. 2016) and for *G. agassizii* (78%; Harless et al. 2009). *Gopherus polyphemus* also showed strong site fidelity in two habitat types (Castellón et al. 2018).

**Home ranges, environmental condition, and territoriality.**—Annual home-range sizes of desert tortoises at Sugarloaf were not affected by drought conditions in contrast to smaller home ranges estimated for *G. agassizii* in a drought year compared to a productive year (Duda et al. 1999). Home ranges across multiple populations of *G. agassizii* also increased loosely with local rainfall (Franks et al. 2011). If reduced annual forage availability during drought was reflected as lower habitat quality, the lack of change in home-range size at Sugarloaf also contrasts with the prediction that

home ranges should increase in size as habitat quality decreases (McLoughlin et al. 2000). A more robust test of this prediction would be a comparison of home-range sizes among tortoise populations across the distribution of the species (or between species) and across a range of regional food abundance and predictability (McLoughlin et al. 2000).

Mean home-range overlap also did not appear to be affected by the degree of drought. These results are opposite the predictions by Maher and Lott (2000) in which overlap among home ranges should be high under conditions with low food abundance, low during moderate conditions, and high again during extremely favorable conditions. A possible explanation is related to the diverse list of perennial trees and shrubs, subshrubs and woody vines, succulents, and perennial grasses in the diet of *G. morafkai* (Van Devender et al. 2004). Despite Sugarloaf experiencing multiple years of substantial drought conditions during the study (e.g., 2002 received only 28% of the long-term mean annual precipitation; Averill-Murray et al. 2018), the Arizona Upland Subdivision of the Sonoran Desert may be productive enough that perennial forage remains moderately abundant even when annual forage is reduced under drier conditions. This is consistent with the prediction of Maher and Lott (2000) that maintaining more exclusive territories is not beneficial with super-abundant food resources.

Harless et al. (2009) concluded that a high degree of MCP overlap in both sexes of *G. agassizii* suggested a lack of territoriality even though both sexes had greater overlap with males than with females, and Castellón et al. (2018) found no differences in overlap between sexes of *G. polyphemus*. Note, though, that static overlap of MCP estimates may be misleading because it does not take into account the individual utilization distributions and may result in large estimates of overlap even though the probability of finding the two animals in the same area is low (Fieberg and Kochanny 2005). Interestingly, gravid *G. morafkai* at Sugarloaf were less likely to overlap annual home ranges with other gravid females than were pairs of non-gravid females. Even though their home-range areas were similar, gravid females spending relatively more time restricted to their nest sites (Murray et al. 1996) might spend less time at the periphery of their home ranges, thereby contributing to a reduced probability of occupying the same area with other similarly restricted gravid females. Additional examination of burrow usage may help further tease apart patterns in space use between *G. morafkai* of different age, sex, and reproductive condition.

**Conclusions.**—Understanding the space requirements and types of movements present in an animal population will influence management actions, such as setting aside

reserves for species that are relatively sedentary in their annual home ranges (Harless et al. 2010; Allen and Singh 2016). Likewise, understanding how resource use and availability affects home ranges can also affect the type of management actions within particular areas (Warrick et al. 1998; Christie et al. 2012). For example, the lack of a relationship between *G. morafkai* home-range size at Sugarloaf and rainfall (along with associated annual plant production) suggests that maintaining or increasing native perennial forage may be an important management tool, especially in an increasingly arid climate. Additional study of home ranges and burrow use will help parse the extent to which habitat capacity is defined by characteristics subject to management, such as vegetation, in comparison to relatively permanent habitat features such as rock shelters.

While focusing management actions solely on home-range size may be relevant and useful in highly fragmented landscapes (e.g., Eubanks et al. 2002), incorporating such localized actions into an ecological network by preserving connectivity for dispersing individuals is especially important for proactive conservation (Allen and Singh 2016). Small effective population sizes of *G. morafkai* suggest that dispersal events probably played an important role in the long-term maintenance of local populations, with microsatellite-based estimates of gene flow ranging from about three to six migrants per generation (Edwards et al. 2004a). Our data revealed a high rate of dispersal of immature tortoises (50% over 10 y), but additional study is needed to document ultimate survival, settlement, and reproductive contribution to new populations, especially in light of the loss of historic dispersal routes as a result of anthropogenic landscape change (Edwards et al. 2004a; Howland and Rorabaugh 2004).

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