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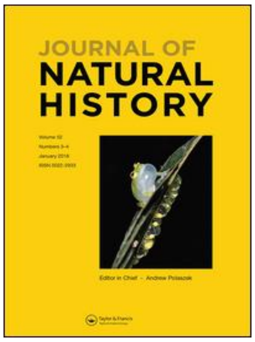

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Life in the thornscrub: movement, home range, and territoriality of the reticulate collared lizard (*Crotaphytus reticulatus*)

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ABSTRACT

Several habitats may be required for an animal's persistence, and movements within and among these habitats characterise an animal's home range. For species of lizards, variation in home range size is typically best explained by either sit-and-wait or active foraging styles. In this study, we explore movements, home range size, and territoriality of Reticulate Collared Lizards (*Crotaphytus reticulatus*) from the typically sit-and-wait foraging subfamily Crotaphytinae. Over three years, we tracked 10 adult males and four adult females using GPS telemetry and found male *C. reticulatus* moved significantly longer distances and maintained significantly larger home ranges and core areas than females. We observed no home range overlap in females and one case of overlap in males, although all females maintained home ranges overlapped by a single male home range. The one-to-one pattern of a male home range overlapping just a single female home range is consistent with male mate guarding observed in active foragers. Moreover, compared to classic sit-and-wait foraging Common Collared Lizards (*C. collaris), C. reticulatus* moves more frequently, maintains a larger home range, is less territorial, and exhibits less sexual dimorphism; all traits of active foraging lizards. Indeed, *C. reticulatus* was observed actively stalking prey throughout its larger home range similar to *G. wislizenii*, which supports previous predictions regarding convergence in active foraging predatory behaviours between the species.

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Introduction

Animal movements are frequently concentrated into core areas during daily activities like resource acquisition, predator avoidance, and mating (Christian and Waldschmidt 1984). Over the lifetime of an animal, several core areas may be required for persistence, and the collection of movements within and among these core areas make up an animal's home range (Rose 1982). Home range size is most often rationalised through energetic requirements related to body size (Reiss 1988). Large animals require more resources and energy for their maintenance than smaller ones, and must range over larger geographical areas than smaller animals with otherwise similar resource requirements (Pianka 2011). Early

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studies supporting this energetic hypothesis showed that larger home ranges were found in mammal and bird species with greater body mass (e.g., Jenkins 1981), but not reptiles (Turner et al. 1969; Rose 1982; Mysterud et al. 2001). Instead, the major conclusion from this early research on the relationship between energetics and home range size in reptiles was that body size, diet, and foraging style were complexly intertwined (Verwaijen and Van Damme 2008).

For species of lizards in particular, variation in home range size appears to be best explained by foraging style (Verwaijen and Van Damme 2008). Two different styles of foraging are typically observed in lizards, sit-and-wait foraging and active foraging (MacArthur and Pianka 1966). Sit-and-wait foragers are mostly sedentary until suitable prey comes within range of an ambush, while active foragers spend most of their time in search of prey. With respect to home range, actively foraging lizards travel farther in search of prey and therefore use more area than comparably sized sit-and-wait lizards that ambush prey (Warrick et al. 1998). In general, entire lizard families share characteristic foraging styles and typically have similar home range sizes (Perry 1999). For example, members of the family Teiidae are considered active foragers with larger home ranges, and Iguanians are identified as sit-and-wait foragers with comparatively smaller home ranges (Cooper et al. 2001; Cooper 2005).

Within the subfamily Crotaphytinae, however, foraging style characteristics are not shared. For example in the genus *Gambelia*, long-nosed leopard lizards (*G. wislizenii*) spend more time actively stalking prey than congeners (Montanucci 1978; McGuire 1996) sometimes travelling more than 200 m in an hour (Pietruszka 1986). In contrast, blunt-nosed leopard lizards (*G. sila*), which were considered a subspecies of *G. wislizenii* for several decades (Montanucci 1970; Jennings 1995), are thought to be primarily sit-and-wait foragers that occasionally stalk prey (Tollestrup 1983; Warrick et al. 1998). By more actively stalking prey, *G. wislizenii* travels farther and has a larger home range (Schorr et al. 2011) than *G. sila* (Warrick et al. 1998; Germano and Rathbun 2016). A similar pattern has also been discussed for the sister genus, *Crotaphytus* (Montanucci 1978). Reticulate collared lizards (*Crotaphytus reticulatus*) are a markedly more active forager than *C. collaris* within the Crotaphytinae (Husak and Ackland 2003). Indeed, *C. reticulatus* has been observed actively stalking prey similar to *G. wislizenii*, confirming previous predictions regarding convergence in predatory behaviours between the species (Montanucci 1971, 1978; Husak and Ackland 2003). Under a parallel rationale, by more actively stalking prey, *C. reticulatus* should travel farther and therefore have a larger home range than *C. collaris* (Baird et al. 1996). Here, we evaluate this hypothesis, and fill knowledge gaps on the natural history of *C. reticulatus*.

Crotaphytus reticulatus is state-listed as threatened in Texas (Hibbitts and Hibbitts 2015) and was recently petitioned and precluded from federal listing under the Endangered Species Act (U.S. Fish and Wildlife Service 2016). The species' geographic distribution is limited to the Tamaulipan biotic province of southern Texas and adjacent Mexico (Figure 1), most of which is privately owned (Garrett et al. 2019). Key conservation concerns for the species are expanded gas and oil extraction (e.g., Eagle Ford Shale play; Pierre et al. 2018; Wolaver et al. 2018a, 2018b) and the proliferation of exotic grasses, such as buffelgrass (*Cenchrus ciliaris*). Dense cover of exotic grasses has been found to decrease abundances of terrestrial lizards (Scott 1996; Germano et al. 2001, 2012). We present the first study of

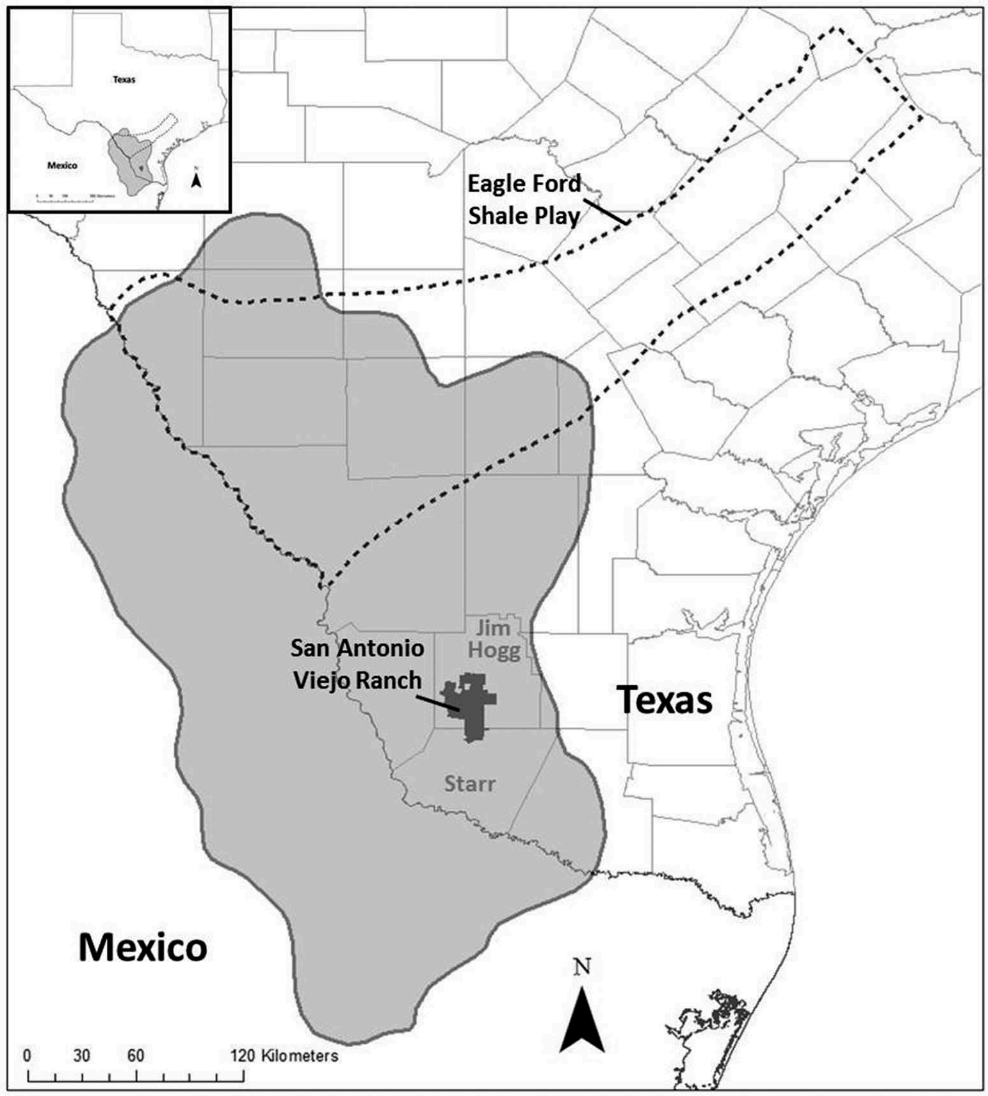

Figure 1. Map of current reticulate collared lizard (*Crotaphytus reticulatus*) distribution (light grey) in Texas and Mexico. The study site (dark grey) was located on the East Foundation's San Antonio Viejo Ranch in Jim Hogg and northern Starr Counties, Texas, USA. Dashed line depicts the Eagle Ford Shale play.

movement and home range size in *C. reticulatus*. From an evolutionary perspective, understanding aspects of movement and home range related to foraging style in *C. reticulatus* is of interest because this species is considered the basal taxon in the genus (McGuire 1996; McGuire et al. 2007) and therefore could help characterise the ancestral state for all *Crotaphytus* (Husak and Ackland 2003). From a conservation perspective, estimates of movement and home range size in *C. reticulatus* can be used to help identify regional conservation priorities and enhance engagement with private landowners, who are the primary stewards for the species.

Materials and methods

Study site

For this study, we selected a site with a known population of *C. reticulatus* located on the San Antonio Viejo Ranch (SAVR) of the East Foundation in Jim Hogg and northern Starr Counties, Texas, USA (Figure 1). This 61,000 ha cattle ranch is a living laboratory dedicated to supporting wildlife conservation and other public benefits of ranching and private land stewardship. Within the ranch boundaries, we frequently observed *C. reticulatus* shuttling between understory light and dark patches while foraging and basking in dense Tamaulipan thornscrub habitat scattered across gravelly hills and loamy flats with characteristic plants of: mesquite (*Prosopis glandulosa*), several species of Acacia (*A. berlandieri, A. rigidula, A. tortuosa*), mimosa (*Albizia julibrissin*), paloverde (*Cercidium macrum*), white brush (*Aloysia lycioides*), cenizo (*Leucophyllum frutescens*), and prickly pear (*Opuntia lindheimeri*). Grasses such as *Bouteloua hirsuta* and *Hilaria* are interspersed within the shrubs and small trees (Garrett et al. 2019).

Telemetry

During June–July 2015 and from March to May 2016–2017, we conducted driving and walking surveys through the site to capture *C. reticulatus* individuals for telemetry. We captured individuals by hand under rocks, by noose during periods of peak activity, and by pitfall trap in one instance. We marked and measured each lizard: we recorded snout-to-vent length (SVL; mm) using a ruler; head width and length using calipers (mm); mass using Pesola® scales (g); and sex for all captured individuals.

We fit individuals >40 g with a telemetry harness, which included both a Global Positioning System (GPS) receiver (Lotek Wireless Inc., Newmarket, Ontario, Canada) and a Very High Frequency (VHF) transmitter (model R1635; Advanced Telemetry Systems Inc., Isanti, Minnesota, USA). We glued the VHF transmitter to the side of the larger GPS receiver with Loctite epoxy, cut and wrapped a thin strip of model plane vinyl around them, and then heat shrunk the VHF transmitter and GPS receiver together. We epoxied hollow spacers to each end of the GPS receiver, and then we used braided fishing line through the holes of the spacers to fasten the harness to the lizard. We tied the anterior end of the telemetry harness around the lizard's waist in front of the back legs, and then we tied the posterior end around the base of the tail (Figure 2). We applied a single drop of super glue to both knots tied around the lizard. Each harness weighed approximately 2.1 g, or at most 5.25% of body mass.

Because this species appears to actively forage throughout much of the day (Husak and Ackland 2003), we programmed the GPS receiver to store positional data on the lizard from GPS satellites at 0700, 1100, 1500, and 1700 hrs. Each GPS receiver stored 50 data points, so at day 12, we relocated lizards using the VHF transmitter and recaptured them. We removed the telemetry harness from each lizard to recharge the GPS receiver and download positional data. During this process, which typically lasted 4 hrs, we placed lizards in cloth bags inside a dark plastic shoebox with air holes. Afterwards, we reattached the telemetry harness to the lizard, and then released the lizard at the point of capture. For movement and home range estimates, we only included positional data points from GPS receivers with a dilution of precision (DOP) < 10 and more than three satellites acquired.

Figure 2. Example of telemetry harness attached to female reticulate collared lizard (*Crotaphytus reticulatus*) in typical Tamaulipan thornscrub habitat found in April 2017 on the East Foundation's San Antonio Viejo Ranch in Jim Hogg and northern Starr Counties, Texas, USA. (Photo credit: W. A. Ryberg).

Data analyses

We used ArcInfo 10.1 (Esri, Redlands, CA) and the adehabitatHR package (Calenge 2006) and ctmm package (Fleming and Calabrese 2019) in R v. 3.5.2 (R Core Team 2018) to calculate the following home range estimators: 100% minimum convex polygons (MCP), 50% core area,95% fixed kernel density estimators (KDE), and autocorrelated kernel density estimator (AKDE). In brief, MCP and 95% KDE represent two different estimates of the total extent of an animal's movements (i.e., home range). In general, MCP has been shown to under predict the home range of animals, and 95% KDE has been shown to over predict. The 50% KDE represents an animal's core area within its home range. Because home range estimators are sensitive to the number of relocations, we only included lizards with at least 24 fixes in the analyses (Stone and Baird 2002). The least-squares cross validation (LSCV) method of selecting the smoothing parameter, recommended by Seaman et al. (1999) failed to minimise the Mean Integrated Squared Error (MISE) for most lizards; therefore we used the reference bandwidth instead. Kernel methods are known to perform poorly in home ranges that contain distinct boundaries (e.g. cliffs, rivers, ponds; Getz et al. 2007). Our study site contained no physical barriers to lizard movements. Sampling lizards four times a day can result in spatial autocorrelation; therefore, we also included an estimate of home range for each individual using autocorrelated kernel density estimation (Fleming et al. 2015). We followed the standard work flow for ctmm recommended by Calabrese et al. (2016) and report the akde for the best fitting model within ΔAIC of 2 that visually fits the variogram. We also calculated step and path length movements, as well as net displacement following Beyer (2004). We calculated percentage overlap of MCPs for all lizards (i.e., male-male, female-female, male-female) in ArcInfo 10.1 (Esri, Redlands, CA) to characterise territoriality of *C. reticulatus*. To test for differences in size, movement and home range estimates for male and female *C. reticulatus*, we conducted t-tests. Movement and home range variables were not normally distributed, so we log transformed data and verified normality and homoscedasticity before conducting analyses. Size data met parametric assumptions of the t-tests. We conducted all statistical analyses in PAST v3.07 (Hammer and Harper 2006).

Results

We observed 47 *C. reticulatus* at SAVR on surveys conducted between June 2015 and June 2017. We captured 28 of these: 10 juveniles, 5 adult females, and 13 adult males. Juveniles were too small to fit with telemetry harnesses averaging 72 mm SVL and 14 g. Adults were much larger averaging 109 mm and 113 mm SVL and 56 g and 63 g for females and males, respectively. We found no significant differences between adult female and male SVL ($t = -0.79$, $P = 0.44$) and mass ($t = -0.95$, $P = 0.36$); however, head width was significantly larger in males ($\bar{x} = 30$ mm) than females ($\bar{x} = 26$ mm; $t = -2.28$, $P = 0.04$). We also observed larger head lengths in males ($\bar{x} = 34$ mm) than females ($\bar{x} = 31$ mm), although the difference was moderately significant ($t = -1.97$, $P = 0.06$).

We chose not to track 1 adult female and 3 adult males that were captured in early spring prior to the known activity season of *C. reticulatus* (Montanucci 1976). The remaining 4 adult females that were fit with telemetry harnesses averaged 108 mm SVL and 51.3 g, while the 10 adult males averaged 112 mm SVL and 61.0 g (Table 1). These lizards yielded a total of 590 fixes with an average of 43 fixes per adult female and 50 per adult male. We excluded two lizards, 1 female and 1 male, from statistical tests for differences in movement and home range between females and males, because we only relocated them 9 and 7 times, respectively (Table 1).

On average, we estimated that *C. reticulatus* females moved 18.8 m between fixes (i.e., step length) and 826.5 m across all fixes (i.e., total path length), and males moved 49.5 m between fixes and 2,740.9 m across all fixes (Table 1). These movements generated average home range sizes of 5,180 m^2 (MCP), 5,937 m^2 (95% KDE), 1,057 m^2 (50% KDE), and 4,847 m^2 (AKDE) for female *C. reticulatus* and average home range sizes of 32,150 m^2 (MCP), 42,571 m^2 (95% KDE), 8,467 m^2 (50% KDE), and 34,739 m^2 (AKDE) for males (Table 1). In statistical tests for differences in movement and home range size between females and males, we found that male *C. reticulatus* moved significantly longer distances between fixes than females (Figure 3(a); $t = -2.18$, $P = 0.05$) leading to significantly larger home ranges (Figure 3(b), MCP, $t = -2.15$, $P = 0.05$; Figure 3(c), 95% KDE, $t = -3.17$, $P = 0.01$) and core areas (Figure 3(d), 50% KDE, $t = -3.83$, $P < 0.01$).

We did not observe any female home range overlap, but all 3 tracked females included in the analyses maintained home ranges that were overlapped by a single male home range. The percent overlap was substantial for 2 of the females (99.7% and 99.0%) and much less for the remaining female (24%), although there was a large discrepancy in the number of fixes for that pair of individuals (69 female vs. 25 male; Table 1). Of the 9 males included in the analyses, we only observed 2 individuals that maintained overlapping

Table 1. Movement parameters for reticulate collared lizards (*Crotaphytus reticulatus*) estimated with GPS telemetry in Jim Hogg and Starr Counties, Texas (2015–17). Column headings are: SVL = snout-to-vent length, SD = standard deviation, MCP = minimum convex polygon, KDE = kernel density estimation, AKDE = autocorrelated kernel density estimation. Abbreviations for sex are: M = male, F = female.

						Step Length (m)			Net Displacement (m)					
Lizard	Sex	SVL (mm)	Mass (g)	Dates	Number Days/ Fixes	Mean	SD	Total Path Length (m)	Mean	SD	MCP Area (m^2)	50% KDE (m^2)	95% KDE (m^2)	AKDE (m^2)
28	F	116	51.5	16 Mar-18 Apr 2016	34/69	21.3	29.5	1,450.7	20.4	21.9	9,965	615	6,215	5,339
40	F	107	47.0	18 May-29 May 2016	12/36	18.5	15.2	647.0	72.7	20.6	2,177	855	4,201	2,760
38	F	105	54.0	19 May-26 May 2016	8/24	16.6	12.9	381.7	28.0	19.1	3,397	1,702	7,394	6,934
103	F	113	53.0	5 Apr-30 Apr 2017	26/9	38.3	19.4	268.4	39.7	25.9	–	–	–	–
Avg.	F	108	51.3	–	20/43	18.8	19.2	826.5	40.4	20.5	5,180	1,057	5,937	5,011
29	M	112	51.0	17 Mar-24 Mar 2016	8/7	28.6	17.2	171.5	45.5	27.2	–	–	–	–
30	M	105	50.5	17 Mar-16 Apr 2016	31/34	36.1	31.2	1,191.4	107.4	65.2	16,264	10,074	39,765	27,296
34	M	115	61.0	27 Apr-11 May 2016	15/40	50.5	39.2	1,970.7	146.7	66.3	31,910	13,183	62,876	45,586
37	M	116	71.0	19 May-2 Jun 2016	15/46	38.3	35.7	1,723.9	47.8	23.7	11,652	4,456	20,247	17,175
36	M	113	61.0	19 May-3 Jun 2016	16/48	45.7	35.4	2,147.5	62.9	30.7	12,304	5,651	23,623	19,766
41	M	121	69.5	3 Jun-27 Jun 2016	25/65	53.6	32.1	3,429.2	40.5	25.8	14,363	4,551	21,496	15,517
26	M	99	47.0	30 Jun-10 Jul 2015	11/25	19.6	15.1	471.2	35.1	13.3	2,442	1,176	5,347	4,753
104	M	120	62.0	7 Apr-30 Apr 2017	24/65	35.7	35.0	2,281.6	105.4	47.4	35,788	12,035	54,430	42,173
106	M	111	69.0	9 Apr-29 Apr 2017	21/47	63.1	42.6	2,901.0	52.0	29.7	19,098	7,648	32,542	23,086
107	M	107	68.0	9 Apr-15 May, 20-31 May 2017	49/84	103.0	84.7	8,551.2	88.2	67.7	145,531	17,426	122,814	98,077
Avg.	M	112	61.0	–	21.5/50	49.5	39.0	2,740.9	76.2	41.0	32,150	8,467	42,571	32,603

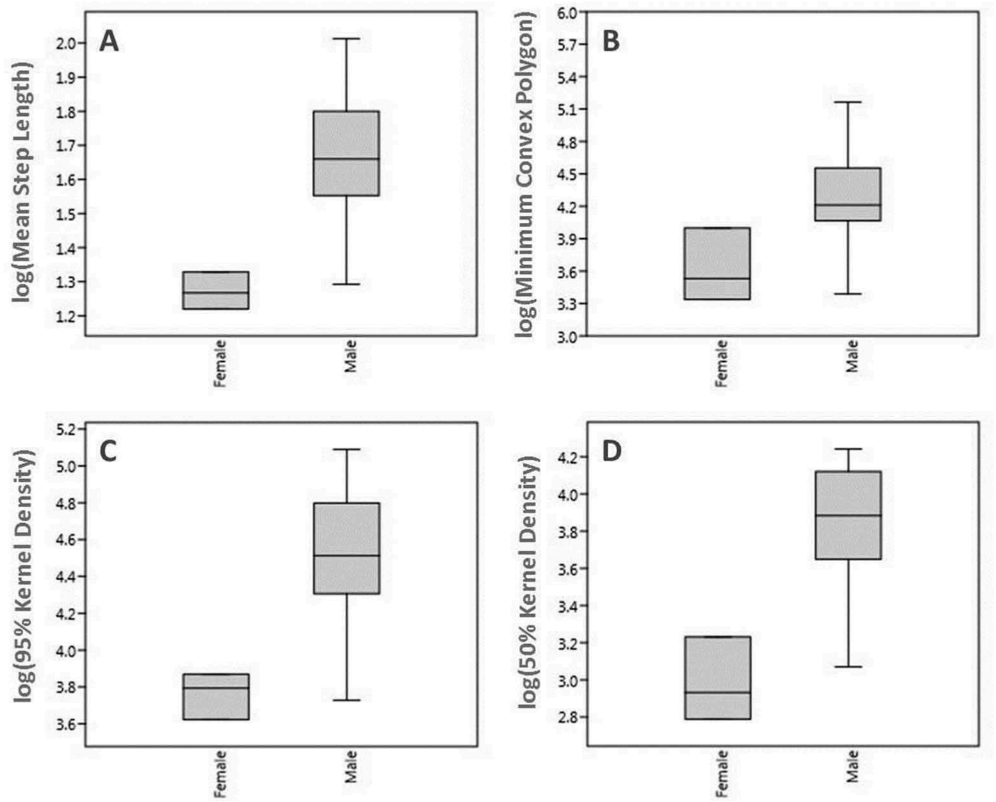

Figure 3. Box plots showing significant differences between log-transformed male and female reticulate collared lizard (*Crotaphytus reticulatus*) (a) Mean step length (m), (b) Minimum convex polygon (m^2), (C) 95% kernel density estimation (m^2), and (D) 50% kernel density estimation (m^2). Movement parameters were estimated with GPS telemetry in Jim Hogg and Starr Counties, Texas (2015–17).

home ranges. Percent overlap for each male was 55% and 28%. While we made efforts to find all individual *C. reticulatus* in the study area, we note that these estimates of home range overlap could be low due to potentially missed individuals.

Discussion

Similar to other members of the Crotaphytidae, we observed that male *C. reticulatus* moved significantly longer distances and maintained significantly larger home ranges and core areas than females (Figure 3, Table 1). Aside from head size, however, we did not find evidence of male-biased sexual size dimorphism in *C. reticulatus*, which is often cited as potentially a causal factor in male-biased home range sizes for the Crotaphytidae and most of the Iguanians (Perry 1999). We only observed male *C. reticulatus* home range overlap in one instance, which suggests the species is somewhat territorial. However, the home range overlap of just a single female in each of 3 male home ranges could suggest that males do not defend multiple female home ranges as seen in congeners like *C. collaris* (Baird et al. 1996). Although additional research is needed for validation, this one-to-one pattern of a male *C. reticulatus* home range overlapping just a single female home range is consistent with male mate guarding or tracking observed in active foragers (Verwaijen and Van Damme 2008).

We also found that average male and female *C. reticulatus* home range size was 25 and 14 times larger than those reported for *C. collaris* males and females, respectively (MCP: male = 1,311 m^2, female = 368 m^2; Baird et al. 1996). Surprisingly, mean step lengths did not vary greatly between these two species, which illustrates that *C. collaris* spends considerable time patrolling or moving back and forth within its smaller home range (Stone and Baird 2002). *Crotaphytus reticulatus*, on the other hand, was observed actively stalking prey throughout its larger home range similar to *G. wislizenii*, which supports previous predictions regarding convergence in active foraging predatory behaviours between the species (Montanucci 1971, 1978; Husak and Ackland 2003). Placing these results in an evolutionary context, *C. reticulatus*, which is considered the basal taxon in the genus (McGuire 1996; McGuire et al. 2007) and therefore could help characterise the ancestral state for all Crotaphytus (Husak and Ackland 2003), appears to move more frequently than *C. collaris*, maintain a larger home range, is less territorial, and exhibits less sexual dimorphism. All of these traits are consistent with active foraging lizards (Tollestrup 1983).

The most likely driver of *C. reticulatus* and *G. wislizenii* convergence in foraging style, movement, and home range size, and lack of territoriality is habitat. Both species occupy habitats comprised of heterogeneous vegetation and sometimes rocks which significantly decrease visibility (Tanner and Krogh 1974; Tollestrup 1983). The degree of visibility within the habitat can influence detection of conspecifics and predators, the mode of communication, the type of colouration, and complexity of displays needed for both advertisement and concealment (Stamps 1983; Tollestrup 1983). When visibility is poor, it is difficult to detect intruders and use displays, so territory defence requires constant patrolling to detect and expel intruders, an energetically expensive activity. Instead, constantly patrolling an area in search of food, or active foraging, is more energy-efficient and appropriate for these two species in this type of habitat. The cryptic dorsal pattern of both species has been identified as a convergent adaptation for efficient predation in habitats where the area beneath the shrubs and cacti is a maze of light and dark shadows produced by sunlight filtering between the branches (Figure 2; Montanucci 1971; Montanucci 1978).

Although research confirming threats to *C. reticulatus* populations and habitat is lacking, much can be inferred from known threats to *G. wislizenii* given the strong convergence in life history between the species. Both species have an affinity for moderate shrub and forb cover with sparse grass cover presumably due to thermoregulatory requirements, preferences for open foraging areas, and a need to limit predation risk (Steffen and Anderson 2006). As such, invasion of exotic grasses is considered a major threat to *G. wislizenii* populations (Scott 1996; Germano et al. 2001, 2012) and, by extension, likely *C. reticulatus* populations as well. In particular, buffelgrass is planted for cattle forage in the lower Rio Grande Valley of southern Texas and northeastern México (Franklin and Molina-Freaner 2010; Tinoco-Ojanguren et al. 2016). The grass is very successful at colonising the open ground between shrubs and trees, which both *G. wislizenii* and *C. reticulatus* require for running during foraging and escape. Thus, controlling the spread of invasive grasses is thought to be a conservation priority for both species. The role of ranching practices in controlling the spread of invasive grasses and thus contributing to wildlife conservation is an important topic of future research.

Crotaphytus reticulatus were thought to be uncommon within their Texas distribution, but populations were believed to be stable over time because habitat was contained within large ranches in south Texas that restricted development (U.S. Fish and Wildlife Service 2016). Moreover, ranching practices in the region have remained unchanged for decades where *C. reticulatus* populations are known to occur (pers. com. T.J. Hibbitts). Although conducted at just a single large ranch, this study supports both of these notions. Populations of *C. reticulatus* on San Antonio Viejo Ranch of the East Foundation appeared robust over the three-year study showing all the signs of annual recruitment (i.e., gravid females and juveniles). However, approximately 25% of the species' range occurs in the Eagle Ford Shale of southern Texas (Figure 1). Expanded gas and oil extraction in this area has the potential to threaten *C. reticulatus* habitat and populations (Pierre et al. 2018; Wolaver et al. 2018a, 2018b). As seen in other lizard species, habitat may be directly lost from development of energy infrastructure (Hibbitts et al. 2013), or *C. reticulatus* populations may be impacted by behavioural avoidance of or direct traffic mortality along the roads interconnecting oil and gas wells (Fahrig and Rytwinski 2009; Hibbitts et al. 2017; Young et al. 2018). Although the exact ways in which energy development will impact *C. reticulatus* populations are unknown, the active foraging style and associated movement, home range, and territoriality traits of this species described here suggest that the effects of energy-driven habitat loss and fragmentation on *C. reticulatus* populations is a topic worthy of future research.

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Disclosure statement

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References

Baird TA, Acree MA, Sloan CL. 1996. Age and gender-related differences in the social behavior and mating success of free-living collared lizards, *Crotaphytus collaris*. Copeia. 1996:336–347. doi:10.2307/1446849.

Beyer HL. 2004. Hawth's analysis tools for ArcGIS. [accessed 2018 Sep 15]. http://www.spatialecology.com/htools.

Calabrese JM, Fleming CH, Gurarie E. 2016. ctmm: an R package for analyzing animal relocation data as a continuous-time stochastic process. Methods Ecol Evol. 2016:1124–1132. doi:10.1111/2041-210X.12559.

Calenge C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model. 197:516–519. doi:10.1016/j.ecolmodel.2006.03.017.

Christian KA, Waldschmidt S. 1984. The relationship between lizard home range and body size: a reanalysis of the data. Herpetologica. 1984:68–75.

Cooper WE. 2005. The foraging mode controversy: both continuous variation and clustering of foraging movements occur. J Zool. 267:179–190. doi:10.1017/S0952836905007375.

Cooper WE, Jr, Vitt LJ, Caldwell JP, Fox SF. 2001. Foraging modes of some American lizards: relationships among measurement variables and discreteness of modes. Herpetologica. 2001:65–76.

Fahrig L, Rytwinski T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecol Soc. 14:1. doi:10.5751/ES-02815-140121.

Fleming CH, Calabrese JM. 2019. ctmm: Continuous-Time Movement Modeling. R package version 0.5.5. [accessed 2019 May 15]. https://CRAN.R-project.org/package=ctmm.

Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM. 2015. Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology. 96:1182–1188. doi:10.1890/14-2010.1.

Franklin K, Molina-Freaner F. 2010. Consequences of buffelgrass pasture development for primary productivity, perennial plant richness, and vegetation structure in the drylands of Sonora, Mexico. Conserv Biol. 24:1664–1673. doi:10.1111/j.1523-1739.2010.01540.x.

Garrett TB, Ryberg WA, Adams CS, Campbell TA, Hibbitts TJ. 2019. Diurnal and nocturnal habitat use in reticulate collared lizards (*Crotaphytus reticulatus*). In press at Southwestern Naturalist.

Germano DJ, Rathbun GB. 2016. Home range and habitat use by blunt-nosed leopard lizards in the southern San Joaquin Desert of California. J Herpetol. 50:429–434. doi:10.1670/15-006.

Germano DJ, Rathbun GB, Saslaw LR. 2001. Managing exotic grasses and conserving declining species. Wildl Soc Bull. 2001:551–559.

Germano DJ, Rathbun GB, Saslaw LR. 2012. Effects of grazing and invasive grasses on desert vertebrates in California. J Wildl Manage. 76:670–682. doi:10.1002/jwmg.316.

Getz WM, Fortmann-Roe S, Cross PC, Lyons AJ, Ryan SJ, Wilmers CC. 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PLoS One. 2:e207. doi:10.1371/journal.pone.0000207.

Hammer Ø, Harper DAT. 2006. Paleontological data analysis. Oxford: Blackwell Publishing.

Hibbitts TD, Hibbitts TJ. 2015. Texas lizards: a field guide. Austin (TX): University of Texas Press.

Hibbitts TJ, Fitzgerald LA, Walkup DK, Ryberg WA. 2017. Why didn't the lizard cross the road? Dunes sagebrush lizards exhibit road-avoidance behaviour. Wildl Res. 44:194–199. doi:10.1071/WR16184.

Hibbitts TJ, Ryberg WA, Adams CS, Fields AM, Lay D, Young ME. 2013. Microhabitat selection by a habitat specialist and a generalist in both fragmented and unfragmented landscapes. Herpetol Conserv Biol. 8:104–113.

Husak JF, Ackland EN. 2003. Foraging mode of the reticulate collared lizard, *Crotaphytus reticulatus*. Southwest Nat. 48:282–286. doi:10.1894/0038-4909(2003)048<0282:FMOTRC>2.0.CO;2.

Jenkins SH. 1981. Common patterns in home range-body size relationships of birds and mammals. Am Nat. 118:126–128. doi:10.1086/283807.

Jennings MR. 1995. Gambelia sila. Catalogue of Amphibians and Reptiles (CAAR). Austin (TX): University of Texas.

MacArthur RH, Pianka ER. 1966. On optimal use of a patchy environment. Am Nat. 100:603–609. doi:10.1086/282454.

McGuire J. 1996. Phylogenetic systematics of crotaphytid lizards (Reptilia: Iguania: Crotaphytidae). Pittsburgh: Carnegie Museum of Natural History.

McGuire JA, Linkem CW, Koo MS, Hutchison DW, Lappin AK, Orange DI, Lemos-Espinal J, Riddle BR, Jaeger JR. 2007. Mitochondrial introgression and incomplete lineage sorting through space and time: phylogenetics of crotaphytid lizards. Evolution. 61:2879–2897. doi:10.1111/j.1558-5646.2007.00239.x.

Montanucci RR. 1970. Analysis of hybridization between *Crotaphytus wislizenii* and *Crotaphytus silus* (Sauria: Iguanidae) in California. Copeia. 1970:104–123. doi:10.2307/1441979.

Montanucci RR. 1971. Ecological and distributional data on *Crotaphytus reticulatus* (Sauria: Iguanidae). Herpetologica. 1971:183–197.

Montanucci RR. 1976. Crotaphytus reticulatus. Catalogue of Amphibians and Reptiles (CAAR). Austin (TX): University of Texas.

Montanucci RR. 1978. Dorsal pattern polymorphism and adaptation in *Gambelia wislizenii* (Reptilia, Lacertilia, Iguanidae). J Herpetol. 1978:73–81. doi:10.2307/1563506.

Mysterud A, Langvatn R, Yoccoz NG, Chr N. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. J Anim Ecol. 2001:915–923. doi:10.1046/j.0021-8790.2001.00559.x.

Perry G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. Am Nat. 153:98–109. doi:10.1086/303145.

Pianka ER. 2011. Evolutionary ecology. New York (NY): Harper Collins College Publishers.

Pierre JP, Wolaver BD, Labay BJ, LaDuc TJ, Duran CM, Ryberg WA, Hibbitts TJ, Andrews JR. 2018. Comparison of recent oil and gas, wind energy, and other anthropogenic landscape alteration factors in Texas through 2014. Environ Manage. 61:805–818. doi:10.1007/s00267-018-1000-2.

Pietruszka RD. 1986. Search tactics of desert lizards: how polarized are they? Anim Behav. 34:1742–1758. doi:10.1016/S0003-3472(86)80261-5.

R Core Team. 2018. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Reiss M. 1988. Scaling of home range size: body size, metabolic needs and ecology. Trends Ecol Evol. 3:85–86. doi:10.1016/0169-5347(88)90025-0.

Rose B. 1982. Lizard home ranges: methodology and functions. J Herpetol. 1982:253–269. doi:10.2307/1563718.

Schorr RA, Lambert BA, Freels E. 2011. Habitat use and home range of long-nosed leopard lizards (*Gambelia wislizenii*) in canyons of the ancients national monument, Colorado. Herpetol Conserv Biol. 6:312–323.

Scott NJ. 1996. Evolution and management of the North American grassland herpetofauna. United States Department of Agriculture Forest Service General Technical Report RM:40-53. Fort Collins, CO: United States Forest Service.

Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA. 1999. Effects of sample size on kernel home range estimates. J Wildl Manage. 1999:739–747. doi:10.2307/3802664.

Stamps JA. 1983. Sexual selection, sexual dimorphism, and territoriality. In: Huey RB, Pianka ER, Schoener TW, editors. Lizard ecology: studies of a model organism. Cambridge (MA): Harvard University Press; p. 169–204.

Steffen JE, Anderson RA. 2006. Abundance of the long-nosed leopard lizard (*Gambelia wislizeni*) is influenced by shrub diversity and cover in southeast Oregon. Am Midl Nat. 156:201–207. doi:10.1674/0003-0031(2006)156[201:AOTLLL]2.0.CO;2.

Stone PA, Baird TA. 2002. Estimating lizard home range: the Rose model revisited. J Herpetol. 36:427–436. doi:10.1670/0022-1511(2002)036[0427:ELHRTR]2.0.CO;2.

Tanner WW, Krogh JE. 1974. Ecology of the leopard lizard, *Crotaphytus wislizeni* at the Nevada test site, Nye County, Nevada. Herpetologica. 1974:63–72.

Tinoco-Ojanguren C, Reyes-Ortega I, Sánchez-Coronado ME, Molina-Freaner F, Orozco-Segovia A. 2016. Germination of an invasive *Cenchrus ciliaris* L. (buffel grass) population of the Sonoran

Desert under various environmental conditions. S Afr J Bot. 104:112–117. doi:10.1016/j.sajb.2015.10.009.

Tollestrup K. 1983. The social behavior of two species of closely related leopard lizards, *Gambelia silus* and *Gambelia wislizenii*. Ethology. 62:307–320.

Turner FB, Jennrich RI, Weintraub JD. 1969. Home ranges and body size of lizards. Ecology. 50:1076–1081. doi:10.2307/1936898.

U.S. Fish and Wildlife Service. 2016. Evaluation of a petition to list the reticulate collared lizard as an endangered or threatened species under the act, FWS–R2–ES–2015–0109. Fed Regist. 81 (51):14068–14069.

Verwaijen D, Van Damme R. 2008. Wide home ranges for widely foraging lizards. Zoology. 111:37–47. doi:10.1016/j.zool.2007.04.001.

Warrick GD, Kato TT, Rose BR. 1998. Microhabitat use and home range characteristics of blunt-nosed leopard lizards. J Herpetol. 1998:183–191. doi:10.2307/1565295.

Wolaver B, Pierre JP, Lebay B, LaDuc T, Duran CM, Ryberg WA, Hibbitts TJ. 2018a. An approach for evaluating changes in land-use from energy sprawl and other anthropogenic activities with implications for biotic resource management. Environ Earth Sci. 77:171. doi:10.1007/s12665-018-7323-8.

Wolaver BD, Pierre JP, Ikonnikova SA, Andrews JR, McDaid G, Ryberg WA, Hibbitts TJ, Duran CM, Labay BJ, LaDuc TJ. 2018b. An improved approach for forecasting ecological impacts from future drilling in unconventional shale oil and gas plays. Environ Manage. 62:323–333. doi:10.1007/s00267-018-1042-5.

Young ME, Ryberg WA, Fitzgerald LA, Hibbitts TJ. 2018. Fragmentation alters home range and movements of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*). Can J Zool. 96:905–912. doi:10.1139/cjz-2017-0048.