Spatial ecology of the Texas Alligator Lizard (*Gerrhonotus infernalis*) in Blanco County, Texas

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ABSTRACT.—Texas Alligator Lizards (*Gerrhonotus infernalis*) range from Central Texas into adjacent northeastern Mexico, and published ecological studies on their terrestrial and arboreal movement patterns are lacking. We used radiotelemetry to assess movements, annual home range, and arboreal activity of *G. infernalis* at Bamberger Ranch Preserve, Blanco County, Texas, to provide baseline ecological data for populations occurring in the northernmost extent of the species' range. Movement patterns were influenced by temporal (e.g., seasonal) and behavioral cues (e.g., breeding period), but generally no differences were observed between sexes. Annual home range varied, but males averaged larger 95% MCP (minimum convex polygon) annual home ranges, while females averaged larger 50% MCP core use areas, although we were unable to test for differences due to low sample sizes. Males and females exhibited similar arboreal trends, but arboreal activity did vary by season and diurnal period. Most arboreal activity occurred during the summer and late spring, with less during the fall and winter months. *Gerrhonotus infernalis*, on average, inhabited higher perch sites during the evening and morning diurnal periods and lower perch sites during the afternoon periods. These findings provide novel insights into the ecology of *G. infernalis* in Central Texas and will aid in future management activities.

RESUMEN.—El Cantil de Tierra (*Gerrhonotus infernalis*) se distribuye desde la parte central del estado de Texas en los Estados Unidos, hasta la zona fronteriza del Noreste de México. La información ecológica publicada formalmente sobre sus patrones de movimiento tanto arbóreos como terrestres es muy escasa y con la finalidad de proveer información ecológica básica sobre las poblaciones existentes en la parte mas al norte de su rango de distribución natural, hemos utilizado radiotelemetria para analizar el área de distribución anual y la actividad arbórea de *G. infernalis* en Bamberger Ranch Preserve, en el condado de Blanco, Texas. De movimiento en *G. infernalis* fueron influenciados por señales ambientales (estaciones) y de comportamiento (periodo de reproducción), pero en términos generales, no se encontraron diferencias entre sexos. El rango anual de distribución espacial fue variable y los machos promediaron un mayor uso total del espacio, mientras que las hembras promediaron un uso mayor de sus áreas de preferencia, aunque dicha diferencia no fue significativa. Machos y hembras presentaron hábitos arbóreos similares, aunque vale destacar que la actividad arbórea presento variaciones estacionales y también durante el periodo diurno. La mayoría de la actividad arbórea ocurrió durante el verano y el fin de la primavera, mostrando una reducción en el final del otoño y el invierno. En promedio, *G. infernalis* utilizo sitios de percha más altos durante las últimas horas de la tarde y las primeras horas de la mañana. Los sitios de percha de menor elevación fueron utilizados durante las primeras horas de la tarde. Los resultados de esta investigación proveen información novedosa acerca de la ecología de la especie en la parte central del estado de Texas y favorecen el desarrollo de nuevas acciones de manejo para la especie.

The spatial ecology of animals can be influenced by specific habitat arrangement, environmental conditions (both biotic and abiotic), distribution of required resources, mates, reproductive habits, competition, and anthropogenic disturbances (Johnston and Frid 2002, Alerstam et al. 2003). Spatial activity can be described as movements established over a certain time frame, such as seasonal activity periods (e.g., spring or fall), reproductive versus nonreproductive periods, or an animal's annual home range (Burt 1943, Brown and Orians 1970). Important resources such as thermoregulatory sites, potential mates, prey composition, and hibernacula often change

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spatiotemporally in distribution, influencing animal movements at different times of the year (Noyce and Garshelis 2011, Balouch et al. 2022). An animal's home range can be considered the entire area traveled by an individual during its regular activities and is commonly rationalized through energetic requirements related to body size: larger animals require greater resources and energy than smaller animals and may have to travel greater distances to obtain needed resources (Burt 1943, Mace and Harvey 1983, Perry and Garland 2002). However, research conducted on the relationship between home range size and energetics in reptiles concluded that diet, body size, and foraging style were intricately intertwined; for lizards in particular, changes in home range extent appear to be best explained by foraging behavior (Verwaijen and Van Damme 2008).

Many lizards are primarily terrestrial, but some exhibit highly arboreal lifestyles, which adds an additional dimension to movement descriptions. Vertical movements within specific habitats can be affected by temperature, seasonality, complexity of microhabitat, predator density, and geography (Melville and Schulte 2001, Barreto-Lima et al. 2013, Muñoz and Losos 2018). Another characteristic of arboreal movements is differential selection in perch height during different diurnal periods. Semiarboreal species can exhibit differing perch dynamics at different activity periods such as inhabiting lower perch sites during higher activity periods or higher perch sites during inactive periods; these perch dynamics are commonly attributed to adaptive strategies for predator avoidance, thermoregulation, or sleeping (Singhal et al. 2007, Ikeuchi et al. 2012).

Texas Alligator Lizards (*Gerrhonotus infernalis*) are members of the Anguidae family, subfamily Gerrhonotinae, and range from Central Mexico into the southern United States (Powell et al 2016). In Texas, they can be found throughout the Edwards Plateau stretching into the Big Bend region, primarily occupying rocky slopes and hillsides, riparian areas, and wooded canyon habitats (Greene et al. 2009). In general, published studies on this species are lacking, which is likely a consequence of their status as a species of least concern (Hammerson et al. 2007) in addition to their cryptic and arboreal nature. Movement patterns are a relatively undocumented characteristic for *G. infernalis* (along with density, territoriality, and home range), but the species is thought to exhibit active or wide foraging habits (Gans and Tinkle 1977, Vitt and Pianka 1994, García Bastida 2013, Yasuda 2015). Studying the movement patterns of *G. infernalis* is critical to developing management plans, as this can identify required habitat types (i.e., overwintering, mating, and nesting sites) and factors limiting abundance and distribution (Rutherford and Gregory 2003, Millar and Blouin-Demers 2011). Only one prior study (García Bastida 2013) has attempted to utilize radiotelemetry to understand the ecological characteristics of *G. infernalis*; occurring near Monterrey, Nuevo León, Mexico, this study indicated that *G. infernalis* is primarily terrestrial, as no arboreal activity was described. Although García Bastida (2013) was an in-depth study, the results do not appear to represent the spatial characteristics seen in Central Texas populations, which exhibit highly arboreal lifestyles (Greene et al. 2009, Ralidis and Acuna 2012).

Thus, our goals were to describe movement patterns and provide baseline ecological data for *G. infernalis* populations occurring in the northernmost extent of the species' range in Central Texas. Our specific objectives for this study were to estimate annual home range and to characterize seasonal variation in fine-scale movements and arboreal activity for *G. infernalis*.

METHODS

Our study was conducted at Selah, Bamberger Ranch Preserve, a 2225-ha ranch located in Blanco County, Texas, approximately 40 miles west of Austin, Texas. The landscape consists of hilly terrain, wooded canyons, savannah grasslands, hardwood slope and motte forests, and riparian hardwood and herbaceous areas. We chose 2 sampling sites on the preserve based on preliminary surveys and year-round availability, as parts of the ranch are leased out for hunting at different periods. The first site was at Turkey Hollow Hill (THH) and the second at Rachel Carson Trail (RCT). The 2 sites are approximately 3 km apart and differ in use, proximity to anthropogenic activities, and vegetation types present. The THH site is approximately 2.76 ha and consists of a north-facing sloped hill with mixed hardwood/juniper slope and motte forests scattered with rock complexes and a top limestone rock outcropping edge. Rachael Carson Trail is smaller (0.63 ha) and consists of a south-facing, primarily oak hardwood slope and riparian forest, with a small west-to-east tapering

rock wall and foot trails; it lies directly adjacent to a paved ranch road.

From 15 April 2021 to 15 May 2022, we conducted walking surveys for *G. infernalis* at both THH and RCT. Once *G. infernalis* individuals were encountered, we captured them either by the pole and lasso method or by hand and recorded the following data for each: sex, mass, snout–vent length (SVL), and tail length (TL). To delineate between individuals, we injected passive integrated transponder (PIT) tags via a needle and syringe through the dorsolateral fold of the lizard. After injection, the lizards were kept for a period (<1 h) to monitor their recovery and then released at the point of capture. We tracked each lizard by attaching a Model R1635 radio transmitter (Advanced Telemetry Systems, Inc., Isanti, MN), or a RECCO tag (RECCO AB Lidingö, Sweden) if the transmitter was >7.5% of the individual's body mass (Knapp and Abarca 2009). A Model R410 VHF receiver (Advanced Telemetry Systems, Inc., Isanti, MN) or an R9 RECCO receiver (RECCO AB Lidingö, Sweden) was used to determine the lizard's exact position. We attached the radio transmitter or RECCO tag on the lizard's dorsum approximately 2 cm anterior to the back limbs by applying cyanoacrylate glue and holding the transmitter or tag in place for 30 s. Next, we stimulated the lizard to inflate the abdomen region and used tan micropore surgical tape (3M, St. Paul, MN) to wrap the lizard 3 times, ensuring that the tape was flush with the dorsolateral folds as suggested by García-Bastida et al. (2012).

To understand seasonal variation in movement patterns, we split seasons into 3-month periods based on the average date of observed behavioral shifts: summer, 10 June–10 September 2021; fall, 10 September–10 December 2021; winter, 10 December–10 March 2022; spring, 10 March–10 June 2022. We tracked *G. infernalis* individuals 2–3 days a week during summer, fall, and spring, but only 1 day a week during the winter season, as movements were rare. To ensure that lizards were tracked during different periods of the day, we randomly assigned lizards to groups to be located either in the morning (07:00–11:30), afternoon (13:00–17:30), or evening (18:30–22:00). Each time an individual was located, we recorded GPS coordinates, height above ground (m), and any relevant behavioral observations. We also recorded the following weather variables: temperature (°C), relative humidity (%), dew point (°C), barometric pressure (Hg) and cloud cover by quarter (e.g., 0%–25%).

All statistical analyses for this study were conducted in R version 4.1.1 (R Core Team 2021) using the integrated development environmental RStudio, version 7.1.554 (RStudio Team 2022). All figures and plots were created using the R package 'ggplot2' (Wickham 2016). We reported all means with one standard error ($\bar{x} \pm$ SE), and all statistical tests were considered significant at $\alpha = 0.05$.

To determine temporal changes in movement characteristics in response to seasonal and behavioral cues, we calculated seasonal movement metrics for all lizards that had been radio-tracked for at least 3 weeks. We used the '*sp*' package (Pebesma and Bivand 2005) to calculate mean distance traveled per week (MDTPW) and the '*adehabitatHR*' package (Calenge 2006) to generate 95% minimum convex polygons (MCPs) to estimate space occupied by an individual per season. We used a 2-way analysis of variance (ANOVA) with Bonferroni-corrected pairwise comparisons to understand the effects of sex and season, and the interaction of sex and season on MDTPW and MCP. If assumptions of normality and homoscedasticity were not met, we used the mean of the log-transformed values. We only included individuals tracked for >3 weeks to analyze MDTPW and individuals with >40 days to analyze MCPs in the 2-way ANOVAs. Due to a smaller sample size and limited tracking data for lizards at RCT in comparison to THH (RCT = 12, THH = 35), we grouped the data from both sites in this analysis.

For each lizard, we also estimated annual home range by generating a 95% MCP and a 50% MCP to estimate core use areas using the '*adehabitatHR*' package (Calenge 2006). Minimum convex polygons are commonly used estimators (due to their simplicity) and work by defining the smallest convex polygon that encloses all locality points of the animal being studied (Nilsen et al. 2008, Boyle et al. 2008). It has been noted that MCPs often overestimate an animal's home range because of the method's inability to distinguish between high- and low-use areas (i.e., sensitivity to extreme outliers) (Powell 2000, Boyle et al. 2008, Silva et al. 2020). To alleviate this overestimation, we employed 95% isopleths to exclude localities that are thought to represent exploratory movements and not part of an animal's true home range (Burt 1943, Silva et al. 2020). We chose to not utilize kernel density

Table 1. Bonferroni-corrected pairwise comparisons for seasonal mean distance traveled per week (MDTPW) and 95% minimum convex polygon (MCP) of Texas Alligator Lizards (*Gerrhonotus infernalis*) at Bamberger Ranch Preserve, Blanco County, Texas. An asterisk (*) denotes nonsignificant results.

	Fall	Spring	Summer
Seasonal MDTPW			
Spring	<0.001	—	—
Summer	*0.168	0.003	—
Winter	<0.001	<0.001	<0.001
Seasonal 95% MCP			
Spring	0.001	—	—
Summer	*0.247	*0.440	—
Winter	<0.001	<0.001	<0.001

estimators as an additional method, due to their inconsistencies in selecting the appropriate smoothing factor as well as problems with autocorrelation when animals inhabit the same location on multiple occasions (Row and Blouin-Demers 2006a). We quantified 95% and 50% MCPs both with repeated consecutive positions included and with repeated consecutive positions removed in order to avoid an overemphasis of a single position by an individual (Silva et al. 2020, Bowers et al. 2021). Long-term radio tracking proved difficult because radios would commonly fall off due to snagging on objects such as branches and greenbrier (*Smilax rotundifolia*). Therefore, we chose to include lizards that had been tracked for at least 100 days between May 2021 and June 2022 in order to better understand this specific spatial characteristic. Due to a low sample size ($n = 7$ males, 5 females) and variability of the data set, we report only the mean and one standard error ($\bar{x} \pm SE$) calculated for all lizards and by sex.

To understand *G. infernalis* arboreal activity, we located lizards at different diurnal periods as described above. Upon relocating each telemetered lizard, we measured their height above ground in meters using a marked rod. Due to the cryptic nature of this species, we were not able to visually observe all lizards upon relocating them; therefore, we only include lizards in the arboreal analysis that were visually located. During daylight saving time (14 March 2021–7 November 2021), we defined evening time as after 18:30; during standard time (7 November 2021–13 March 2022), we defined evening time as after 16:30. We employed Wilcoxon rank-sum tests to test for differences in arboreal height by sex for each season and then used the Kruskal–Wallis rank sum test to look at the effect of

season and diurnal period on arboreal activity. We included every lizard encounter in this specific analysis (i.e., even those with <21 days tracked). No single lizard made up a significant percentage of seasonal localities (median = 4.10%, max = 10.69%) or localities by diurnal period (median = 1.28%, max = 7.87%), thus reducing the likelihood of bias (Row and Blouin-Demers 2006b, Sprague 2017). Because a smaller sample size of localities was retained in this analysis from RCT in comparison to THH (RCT = 103, THH = 569), we grouped the data from both sites.

Results

We captured a total of 54 lizards during this study: 27 males (mean SVL: 134.4 ± 18.6 mm), 24 females (mean SVL: 138.2 ± 14.0 mm), and 3 unsexed juveniles (mean SVL: 73.0 ± 20.2 mm). We did not include 7 individuals in the spatial analysis ($n = 2$ males, 2 females, 3 juveniles) because they were either captured at a different site during preliminary surveys or were too small to safely outfit with radios or RECCO tags. In total, we attempted to track 35 lizards at THH ($n = 19$ males, 16 females) and 12 at RCT ($n = 6$ males, 6 females), resulting in 927 recorded lizard localities (mean per lizard = 18.6 localities, range 1–64 localities). Time of attachment varied by individual and transmitter device and consisted of 55 radio attachment attempts ($\bar{x} = 30.9$ days, range 7–82 days) and 16 RECCO tag attempts ($\bar{x} = 94.0$ days, range 7–219 days). As indicated, the RECCO tag proved better at long-term attachment due to its low profile and ability to lie flush with the dorsum of the lizard. Although this detecting method lasted longer, it was more difficult to locate lizards with this method, as a clear line of sight from the RECCO receiver to the RECCO tag only offered a detectable range of about 15–20 m; this range was further reduced if a lizard was obstructed by an object (e.g., rock crevice or tree hollow). Radio or RECCO tag detachments resulted primarily from snagging on objects such as branches and greenbrier or from falling off after the lizard had shed.

The 2-way ANOVA indicated a significant effect of season on MDTPW ($P \leq 0.001$), but there was no significant effect of sex ($P = 0.880$) or the interaction of season and sex on MDTPW ($F_{3, 57} = 1.362$, $P = 0.263$). The only nonsignificant pairwise comparison of MDTPW by season

TABLE 2. Average seasonal movement metrics for terrestrial and arboreal height of Texas Alligator Lizards (*Gerrhonotus infernalis*) at Bamberger Ranch Preserve, Blanco County, Texas. *NA* indicates movement metrics with insufficient locality points to estimate. Means are presented with standard errors ($\bar{x} \pm$ SE).

Movement metric	Sex	Summer	Fall	Winter	Spring
MDTPW (m)	M	15.1 ± 2.69 (*n* = 8)	36.0 ± 7.06 (*n* = 11)	1.7 ± 0.89 (*n* = 7)	15.3 ± 5.15 (*n* = 8)
	F	17.6 ± 3.18 (*n* = 8)	35.2 ± 7.50 (*n* = 11)	0.34 ± 0.23 (*n* = 4)	4.6 ± 1.42 (*n* = 8)
	All	16.5 ± 2.04	35.2 ± 5.06	1.2 ± 0.59	9.9 ± 2.92
Seasonal 95% MCP (m²)	M	597.0 ± 206.83 (*n* = 4)	7316.0 ± 4680.72 (*n* = 5)	NA (*n* = 6)	891.0 ± 510.98 (*n* = 7)
	F	686.0 ± 356.85 (*n* = 3)	3626.2 ± 2288.71 (*n* = 5)	NA (*n* = 4)	115.0 ± 54.64 (*n* = 4)
	All	635.1 ± 175.34	5471.3 ± 2532.01	NA	608.5 ± 337.54
Arboreal height (m)	M	1.1 ± 0.07 (*n* = 200)	0.63 ± 0.07 (*n* = 167)	0.10 ± 0.03 (*n* = 92)	0.56 ± 0.08 (*n* = 84)
	F	0.86 ± 0.09 (*n* = 130)	0.61 ± 0.08 (*n* = 162)	0.07 ± 0.05 (*n* = 33)	0.39 ± 0.09 (*n* = 59)
	All	1.0 ± 0.06	0.62 ± 0.05	0.09 ± 0.03	0.49 ± 0.06

was between the summer and fall season ($P = 0.168$) (Table 1), despite MDTPW being twice as long during the fall ($\bar{x} = 35.2 \pm 5.06$ m) than in the summer ($\bar{x} = 16.5 \pm 2.04$ m) (Table 2). The winter season included the lowest movement rates observed ($\bar{x} = 1.2 \pm 0.59$ m). Spring was the only season for which a difference in MDTPW was evident between males ($\bar{x} = 15.3 \pm 5.15$ m) and females ($\bar{x} = 4.6 \pm 1.42$ m), but the difference was not statistically significant ($W = 14$, $P = 0.064$).

The 2-way ANOVA indicated a significant effect of season on 95% MCPs ($P = < 0.001$), but there was no significant effect of sex ($P = 0.469$) or the interaction of season and sex on 95% MCPs ($F_{3, 30} = 0.211$, $P = 0.887$). The only nonsignificant pairwise comparisons of 95% MCPs by season were between the summer and fall season ($P = 0.247$) and the summer and spring season ($P = 0.440$) (Table 1), despite the large differences seen between the fall ($\bar{x} = 5471.3 \pm 2532.01$ m) and summer ($\bar{x} = 635.1 \pm 175.34$ m) seasons (Table 2). All winter 95% MCPs for both males and females were 0 m², or not applicable (NA); there were not enough unique localities to estimate 95% MCPs. By 15 December 2021, all lizards had returned to the rocky slope areas and remained relatively static within or just outside their respective overwintering locations until 10 March 2022. Spring was again the only season where a noticeable difference in 95% MCP occurred with males ($\bar{x} = 891.0 \pm 510.98$ m²), who occupied much more space than did females ($\bar{x} = 115.0 \pm 54.64$ m²) (Table 2).

From May 2021 to June 2022, 13 lizards ($n = 8$ males, 5 females) were radio-tracked for 100 days or more and through at least some portion of 2 seasons; the duration of tracking ranged from 101 to 260 days (Table 3). Both 95% and 50% MCP estimates were altered, depending on whether consecutive repeats were retained or not (i.e., MCP estimates increased, decreased, or stayed the same). When consecutive repeats were retained in the analysis, one male lizard (ID 126) had an estimated 50% MCP of 0 m² (marked as NA). This result occurred because the lizard remained static for over 50% of the 219 days that it was tracked—i.e., the 121 days between 30 November 2021 and 30 March 2022. Thus, we report numbers with consecutive relocations removed. The mean 95% MCP annual home range averaged 4663.6 ± 1760.59 m² (range 25.1–22,077.2 m²) for all lizards. Males had a higher average annual 95% MCP (5159.2 ± 2532.46 m²) in comparison to females (3870.7 ± 2442.34 m²). However, females had a larger average 50% MCP (1305.5 ± 982.09 m²) in comparison to males (693.8 ± 304.63 m²). Of the 13 lizards included in this analysis, only 2 were not tracked during the fall season, resulting in a much lower estimation for both measurements (male ID 155: 95% MCP = 181.34 m², 50% MCP = 3.20 m²; female ID 153: 95% MCP = 25.07 m², 50% MCP = 1.07 m²) in comparison to the other lizards tracked (Table 3). While there was much variation in the home range estimates, it appears that the fall breeding season accounts for much of the annual home range size for both males and females.

TABLE 3. Estimated 95% and 50% annual MCPs for both male and female Texas Alligator Lizards (*Gerrhonotus infernalis*) at Bamberger Ranch Preserve, Blanco County, Texas, from May 2021 to June 2022. MCP units are reported in square meters (m^2) and include estimates with and without consecutive locations. X's represent seasons during which an individual was tracked through for some portion, and *NA* represents a movement metric with insufficient unique locality points to estimate.

ID	Sex	Days tracked	Consecutive repeats retained 95% MCP	Consecutive repeats retained 50% MCP	Consecutive repeats removed 95% MCP	Consecutive repeats removed 50% MCP	Summer 2021	Fall 2021	Winter 2021/22	Spring 2022
152	M	162	2266	238	2684	238	X	X		
108	M	260	22,077	662	22,077	2275	X	X	X	
111	M	217	2588	1666	2654	267	X	X	X	X
126	M	219	4841	NA	4970	210		X	X	X
65	M	222	6572	243	6572	1822		X	X	X
91	M	107	1757	171	1409	601	X	X		
72	M	119	726	427	726	134		X	X	
155	M	133	181	3	181	3		X	X	X
74	F	127	13,318	2728	13,317	5188	X	X	X	
109	F	226	2865	540	3381	821		X	X	X
153	F	198	25	1	25	1			X	
132	F	101	2544	577	2306	465	X	X		
150	F	107	200	47	323	52	X	X		

For arboreal activity, we collected 927 localities (n = 543 male, 384 female) ranging in height from 0 to 5.4 m above the ground between May 2021 and June 2022. The percentage of lizard relocations that were >0 m per season were 55.1%, 44.4%, 9.9%, and 37.9% for summer 2021, fall 2021, winter 2021/2022, and spring 2022, respectively. There was a significant effect of season on arboreal activity (χ^2 = 119.23, df = 3, $P \leq 0.001$), with the highest average arboreal height occurring during the summer (1.02 ± 0.06 m) and the lowest occurring during the winter (0.09 ± 0.03 m) (Fig. 1, Table 2). Males were found higher off the ground during summer (W = 10916, P = 0.011) and spring (W = 1966, P = 0.020) seasons, but no differences by sex were evident for the fall (W = 13290, P = 0.768) or winter (W = 1447, P = 0.4398). For the effects of diurnal period on arboreal activity, we collected 234, 431, and 262 observations for the morning, afternoon, and evening periods, respectively. Overall, there was a significant effect of diurnal period on arboreal activity (χ^2 = 77.574, df = 2, P = < 0.001) with both the average morning (0.81 ± 0.07 m) and evening (0.94 ± 0.06 m) arboreal heights being greater than afternoon (0.43 ± 0.04 m) arboreal height (Fig. 1).

DISCUSSION

Gerrhonotus infernalis did exhibit shifts in movement patterns in response to seasonal and behavioral cues. We observed dissimilar trends between sexes in some aspects of their movement ecology, specifically movements during the spring season and some aspects of arboreal activity within seasons, but few differences were statistically significant. Thus, *G. infernalis* appears to be behaviorally similar between sexes in terms of terrestrial and arboreal activity across the year. *Gerrhonotus infernalis* movements during the summer consisted more of ascending and descending vegetation (i.e., perching in the same tree clumps for multiple days), but individuals would generally move to a new location every week. The warm summer season can be considered a period of low energy expenditure for *G. infernalis*, and this common behavior has been documented in reptiles to preserve energy, reduce water loss, and minimize predation risks during hot and dry periods (Christian and Green 1994, Aragón et al. 2001, Ariano-Sánchez et al. 2020).
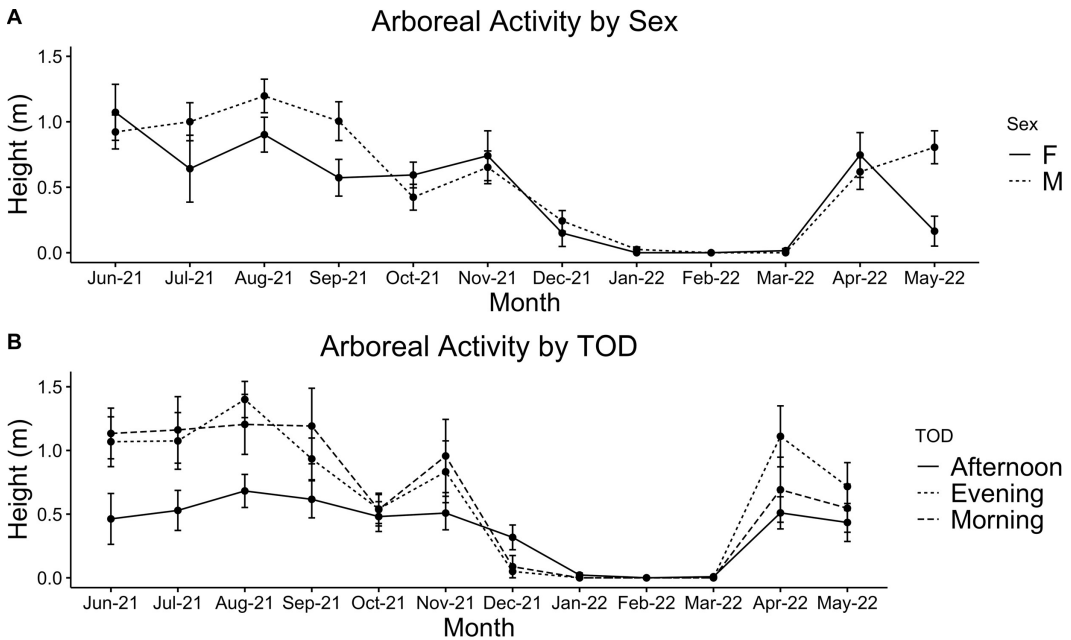
Fig. 1. Texas Alligator Lizards (*Gerrhonotus infernalis*) at Bamberger Ranch Preserve, Blanco County, Texas. *A,* Average monthly arboreal height by sex. *B,* Average monthly arboreal height by time of day (TOD).

Fall is the breeding season for *G. infernalis*, when lizards are typically more active (Aragón et al. 2001, Stark et al. 2005, Castañeda et al. 2007), and both MDTPW and 95% MCPs were greatest during this period. By mid-September, both male and female lizards started moving away from their commonly used summer locations, signaling a shift to the reproductive season. *Gerrhonotus infernalis* movements increased in October, with most individuals found on the ground and moving daily. This increase in movement and area occupied during the mating season has been attributed in other lizards such as *Sceloporus jarrovii*, *S. undulatus*, and *Lacerta monticola* to be a function of reproductive effort, affording more opportunities to find mates (Ferner 1974, Ruby 1978, Aragón et al. 2001). Lizards were tracked across roads and through unanticipated habitat types such as the savannah grassland adjacent to their normally occupied oak/hardwood rocky slope forests at both sites. The drive to copulate appears to push *G. infernalis* lizards through previously undocumented or unexplored habitat types in search of potential mates.

During the winter, activity decreased, with minimal movements only observed during the latter half of December, signaling the end of mating season. Lizards remained relatively static within or just outside of their overwintering sites if unusually warm and sunny days occurred. Retreating to underground refuge during winter months is a common behavior in reptilian species to reduce metabolic activity and depletion of energy reserves; some species may reduce activity for long periods, while others reduce activity only minimally and may resurface to bask when favorable conditions are present (Congdon et al. 1982, Nordberg and Cobb 2016, Cecchetto et al. 2019).

Spring emergence from overwintering sites varied by lizard, but the earliest individuals began exiting by 10 March 2022. The arboreal perching and weekly movement activity that we observed during the summer season did not begin to occur again until April. Spring emergence in reptiles is generally thought to be regulated by ambient and ground temperatures (Lutterschmidt et al. 2006); therefore, it is likely that *G. infernalis* exhibits earlier or later emergence times dependent on region-specific climate factors. Spring was the only season during which males and females had different movement patterns; males made larger movements and consequently had larger activity areas in comparison to females. These differences in movements could be a consequence of the brooding season occurring in spring, as females have been

documented to lay and guard eggs between March and June (Greene et al. 2009, Fielder et al. 2022). One female was confirmed gravid and exhibited low activity; therefore, it is plausible that more of the spring movements for females consist of searching out adequate egg-laying sites within rocky complexes, which could occur at or near their overwintering locations.

Males on average had larger annual home ranges (i.e., 95% MCP), but females averaged larger core use areas (i.e., 50% MCP). Due to the low sample size and wide range of estimates, it cannot be concluded that significant differences occur between sexes. However, there was a similar tendency for males to exhibit greater activity areas as documented in García Bastida (2013). Annual home range estimates are rare for anguid lizards, but males occupying larger areas is a common trend among the Autarchoglossa and Iguania clades (Perry and Garland 2002). Studies suggest that a larger space used by males is determined by availability of females and the potential to increase reproductive success, whereas females may occupy smaller areas and have space determined more by energetic needs (Salvador and Veiga 2001, Perry and Garland 2002). Increasing the sample size and duration of tracking would aid in understanding sexual differences and seasonal effects on annual home range estimates for *G. infernalis*. Only 2 lizards included in the annual home range were not tracked through the fall breeding season and subsequently had the smallest male and female estimates compared to all other lizards tracked. García Bastida (2013) estimated home range of *G. infernalis* by reproductive (fall) and nonreproductive (spring, summer, and winter) periods and found no significant differences (i.e., space occupied during the fall was comparable to the combined space utilized for the summer, winter, and spring seasons). Our study does align with their results in that the fall breeding season contained a substantial amount of the annual movement made by *G. infernalis*.

Seasonally, *G. infernalis* exhibited high arboreal activity in the later spring and summer, but arboreal activity decreased throughout the fall breeding season (when lizards were actively mate searching) and during winter and early spring (when lizards were primarily overwintering in rocky refuge). Seasonal shifts in arboreal activity can be influenced by weather (e.g., temperature, moisture), prey availability, foraging, and behav-ioral cues (e.g., mating) (García et al. 2010). García Bastida (2013) indicated a more terrestrial lifestyle for *G. infernalis* in Nuevo Leon, Mexico; thus, arboreal activity is likely affected by region-specific environmental factors. This intraspecies variation in arboreal activity as a function of geography has been documented in *Anolis* and *Sceloporus* lizards, wherein low-elevation populations were observed to be more arboreal, while higher-elevation populations were observed to be more ground-dwelling; this behavior was considered an adaptive strategy to conform to region-specific thermal variation (Muñoz and Losos 2018).

Arboreal activity was prevalent during the day, except in the winter season, with *G. infernalis* moving to varying perch heights; however, by evening most individuals perched higher up and remained relatively inactive through the night and into the morning, unless disturbed by a passing animal (personal observation). It has been documented that animals are more likely to survive and reproduce when selecting safer locations and conditions for periods of inactivity (Lima and Dill 1990). Studies of arboreality in *Gerrhonotus* are relatively nonexistent, but this shifting in perch height at different diurnal periods is likely related to thermoregulation or antipredator strategies, a common tactic observed in many diurnal species (Muñoz and Losos 2018, Mohanty et al. 2022).

Our results indicate that both terrestrial and arboreal movements in populations of *G. infernalis* in Central Texas are influenced by seasonal and behavioral cues. The observed seasonal changes are similar to those seen in other semiarboreal species inhabiting temperate and tropical environments. Thus, the seasonal patterns documented here represent behavioral strategies that allow *G. infernalis* to take advantage of spatiotemporally fluctuating resources. Our findings are similar to García Bastida (2013) in that both males and females exhibit similar annual home range estimates, but different in that populations of *G. infernalis* in the northernmost extent of the species' range exhibit highly arboreal lifestyles. This information provides valuable insights into the ecology of *G. infernalis*, but there is a need for longer-duration tracking studies to better understand annual home ranges of these lizards. It should be noted that the average recorded temperature across the summer 2021 season was 28.1 °C in Blanco County, Texas, with ample rainfall between the

months of June and July. Thus, it is possible that less movement and arboreal activity could occur during a warmer and drier summer season.

LITERATURE CITED

ALERSTAM, T., A. HEDENSTROM, AND S. AKESSON. 2003. Long-distance migration: evolution and determinants. Oikos 103:247–260.

ARAGÓN, P., P. LOPEZ, AND J. MARTIN. 2001. Seasonal changes in activity and spatial and social relationships of the Iberian Rock Lizard *Lacerta monticola*. Canadian Journal of Zoology 79:1965–1971.

ARIANO-SÁNCHEZ, D., R.M. MORTENSEN, AND S. REINHARDT. 2020. Escaping drought: seasonality effects on home range, movement patterns and habitat selection of the Guatemalan Beaded Lizard. Global Ecology and Conservation 23:e01178.

BALOUCH, S., D.A. DRISCOLL, A. NASEER, M. RAIS, AND T.S. DOHERTY. 2022. Impacts of land cover on reptile movement and habitat use in farming landscapes. Animal Conservation 25:837–848.

BARRETO-LIMA, A.F., E.D.O. PIRES, AND B.M. DE SOUSA. 2013. Activity, foraging mode, and microhabitat use of *Enyalius perditus* (Squamata) in a disturbed Atlantic rainforest in southeastern Brazil. Salamandra 49:177–185.

BOWERS, B.C., D.K. WALKUP, T.J. HIBBITTS, P.S. CRUMP, W.A. RYBERG, A.M. LAWING, AND R.R. LOPEZ. 2021. Should I stay or should I go? Spatial ecology of the Western Chicken Turtles (*Deirochelys reticularia miaria*). Herpetological Conservation and Biology 16:594–611

BOYLE, S.A., W.C. LOURENCO, L.R. DA SILVA, AND A.T. SMITH. 2008. Home range estimates vary with sample size and methods. Folia Primatologica 80:33–42.

BROWN, J.L., AND G.H. ORIANS. 1970. Spacing patterns in mobile animals. Annual Review of Ecology, Evolution, and Systematics 1:239–262.

BURT, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

CALENGE, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

CASTAÑEDA, G., H. GADSDEN, A.J. CONTRERAS-BALDERAS, AND C. GARCÍA-DE LA PEÑA. 2007. Variation in home range of the Side-Blotched Lizard, *Uta stejnegeri*, in Coahuila, Mexico. Southwestern Naturalist 52:461–467.

CECCHETTO, N.R., S.M. MEDINA, S. TAUSSIG, AND N.R. IBARGUENGOYTIA. 2019. The lizard abides: cold hardiness and winter refuges of *Liolaemus pictus argentinus* in Patagonia, Argentina. Canadian Journal of Zoology 97:773–782.

CHRISTIAN, K., AND B. GREEN. 1994. Seasonal energetics and water turnover of the Frillneck Lizard, *Chlamydosaurus kinigii*, in the wet-dry tropics of Australia. Herpetologica 50:274–281.

CONGDON, J.D., A.E. DUNHAM, AND D.W. TINKLE. 1982. Energy budgets and life histories of reptiles. Pages 233–271 *in* C. Gans and F.H. Pough, editors, Biology of the Reptilia. Volume 13. Academic Press, Cambridge, MA.

FERNER, J.W. 1974. Home range size and overlap in *Sceloporus undulatus erythroceilus* (Reptilia: Iguanidae). Copeia 1974:332–337.

FIELDER, C.M., J. HOLMES, AND T.J. HIBBITTS. 2022. *Gerrhonotus infernalis* (Texas Alligator Lizard). Nesting behavior. Herpetological Review 53:132–133.

GANS, C., AND D.W. TINKLE. 1977. Biology of the Reptilia: ecology and behavior. Volume 7. Academic Press, Inc., New York, NY.

GARCÍA, A., M. VALTIERRA-AZOTLA, AND B.C. LISTER. 2010. Behavioral responses to seasonality by two sceloporine lizard species from a tropical dry forest. Animal Biology 60:97–113.

GARCÍA BASTIDA, M. 2013. Ecological aspects of *Gerrhonotus infernalis* (Sauria: Anguidae) in the Chipinque Ecological Park, San Pedro Garza García, Nuevo Leon, Mexico. Doctoral dissertation, Autonomous University of Nuevo Leon, San Nicolás de los Garza, Nuevo Leon, Mexico. 100 pp.

GARCÍA-BASTIDA, M., C.A. MADRID-SOTELO, AND D. LAZCANO. 2012. Evaluation of a simple method of externally attaching radio-transmitters to the Texas Alligator Lizard, *Gerrhonotus infernalis*. Herpetological Review 43:410–412.

GREENE, H.W., P.M. RALIDIS, AND E.W. ACUNA. 2009. Texas Alligator Lizard *Gerrhonotus infernalis* Baird, 1859 "1858." Pages 492–495 *in* L.C. Jones and R.E. Lovich, editors, Lizards of the American Southwest. Rio Nuevo Publishers, Tucson, AZ.

HAMMERSON, G.A., J. VAZQUEZ DIAZ, H. GADSDEN, G.E. QUINTERO DIAZ, P. PONCE-CAMPOS, AND P. LAVIN. 2007. *Gerrhonotus infernalis*. The IUCN Red List of Threatened Species 2007:e.T63707A12707760. https://doi.org/10.2305/IUCN.UK.2007.RLTS.T63707A12707760.en

IKEUCHI, I., M. HASEGAWA, AND A. MORI. 2012. Characteristics of sleeping sites and timing of departure from them in a Madagascan diurnal gecko, *Lygodactylus tolampyae*. Current Herpetology 31:107–116.

JOHNSTON, B., AND L. FRID. 2002. Clearcut logging restricts the movement of terrestrial Pacific Giant Salamanders (*Dicamptodon tenebrosus* Good). Canadian Journal of Zoology 80:2170–2177.

KNAPP, C.R., AND J.G. ABARCA. 2009. Effects of radio transmitter burdening on locomotor ability and survival of iguana hatchlings. Herpetologica 65:363–372.

LIMA, S.L., AND L.M. DILL. 1990. Behavioral decisions made under the risk of predation; a review and prospectus. Canadian Journal of Zoology 68:619–640.

LUTTERSCHMIDT, D.I., M.P. LEMASTER, AND R.T. MASON. 2006. Minimal overwintering temperatures of Red-sided Garter snakes (*Thamnophis sirtalis parietalis*): a possible cue for emergence? Canadian Journal of Zoology 84:771–777.

MACE, G.M., AND P.H. HARVEY. 1983. Energetic constraints on home-range size. American Naturalist 121:120–132.

Melville, J., and J.A. Schulte II. 2001. Correlates of active body temperatures and microhabitat occupation in nine species of central Australian agamid lizards. Austral Ecology 26:660–669.

Millar, C.S., and G. Blouin-Demers. 2011. Spatial ecology and seasonal activity of Blanding's Turtles (*Emydoidea blandingii*) in Ontario, Canada. Journal of Herpetology 45:370–378.

Mohanty, N.P., C. Wagener, A. Herrel, and M. Thaker. 2022. The ecology of sleep in non-avian reptiles. Biological Reviews 97:505–526.

Muñoz, M.M., and J.B. Losos. 2018. Thermoregulatory behavior simultaneously promotes and forestalls evolution in a tropical lizard. American Naturalist 191:E15–E26.

Nilsen, E.B., S. Pedersen, and J.D.C. Linnell. 2008. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecological Research 23:635–639.

Nordberg, E.J., and V.A. Cobb. 2016. Midwinter emergence in hibernating Timber Rattlesnakes (*Crotalus horridus*). Journal of Herpetology 50:203–208.

Noyce, K.V., and D.L. Garshelis. 2011. Seasonal migration of black bears (*Ursus americanus*): causes and consequences. Behavioral Ecology and Sociobiology 65:823–835.

Pebesma, E.J., and R.S. Bivand. 2005. Classes and methods for spatial data in R. R News 5:9–13.

Perry, G., and T. Garland Jr. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. Ecology 83:1870–1885.

Powell, R.A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 *in* L. Boitani and T.K. Fuller, editors, Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, NY.

Powell, R., R. Conant, and J.T. Collins. 2016. Peterson field guide to reptiles and amphibians of eastern and central North America. HarperCollins Publishers, New York, NY.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Ralidis, P., and E. Acuna. 2012. Natural history observations of the anguid lizard *Gerrhonotus infernalis* (Baird, 1859) in Travis County, Texas (Lacetilia: Anguidae). Southwestern Center for Herpetological Research Bulletin 2:3–6.

Row, J.R., and G. Blouin-Demers. 2006a. Kernels are not accurate estimators of home-range size for herpetofauna. Copeia 2006:797–802.

Row, J.R., and G. Blouin-Demers. 2006b. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. Ecoscience 13:443–450.

RStudio Team. 2022. RStudio: integrated development for R. RStudio, Inc., USA. https://www.rstudio.com/

Ruby, D.E. 1978. Seasonal changes in the territorial behavior of the iguanid lizard *Sceloporus jarrovi*. Copeia 1978:430–438.

Rutherford, P.L., and P.T. Gregory. 2003. Habitat use and movement patterns of Northern Alligator Lizards (*Elgaria coerulea*) and Western Skinks (*Eumeces skiltonianus*) in southeastern British Columbia. Journal of Herpetology 37:98–106.

Salvador, A., and J.P. Veiga. 2001. Male traits and pairing success in the lizard *Psammodromus algirus*. Herpetologica 57:77–86.

Silva, I., M. Crane, B.M. Marshall, and C.T. Strine. 2020. Reptiles on the wrong track? Moving beyond traditional estimators with dynamic Brownian bridge movement models. Movement Ecology 8:1–13.

Singhal, S., M.A. Johnson, and J.T. Ladner. 2007. The behavioral ecology of sleep: natural sleeping site choice in three *Anolis* lizard species. Behaviour 144:1033–1052.

Sprague, T.A. 2017. Microhabitat and movement assessment for Northern Mexican Gartersnakes (*Thamnophis eques megalops*) at Bubbling Ponds Hatchery, Arizona. Master's thesis, Arizona State University, Tempe, AZ. 71 pp.

Stark, R.C., S.F. Fox, and D.M. Leslie Jr. 2005. Male Texas Horned Lizards increase daily movements and area covered in spring: a mate searching strategy? Journal of Herpetology 39:169–173.

Verwaijen, D., and R. Van Damme. 2008. Wide home ranges for widely foraging lizards. Zoology 111:37–47.

Vitt, L.J., and E.R. Pianka, editors. 1994. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, NJ. 416 pp.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. https://ggplot2.tidyverse.org

Yasuda, C.M. 2015. Ecology and distribution of the Panamint Alligator Lizard (*Elgaria panamintina*). Master's thesis, California State University, Chico, CA. 67 pp.