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Habitat use of the Texas Alligator Lizard (*Gerrhonotus infernalis*) in Central Texas

Corey M. Fielder[a], Wade A. Ryberg[a], Danielle K. Walkup[a], Jared M. Holmes[b] and Toby J. Hibbitts[a,c]

[a]Texas A&M Natural Resources Institute, College Station, Texas, USA; [b]Origin Ranch, Dripping Springs, Texas, USA; [c]Biodiversity Research and Teaching Collections, Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas, USA

ABSTRACT

Texas alligator lizards (*Gerrhonotus infernalis*) are regionally distributed from Central Texas into adjacent north-eastern Mexico and, apart from field observations, there are few published ecological studies. We utilised radiotelemetry data to assess seasonal macro- and microhabitat as well as arboreal habitat use for *G. infernalis* at two sites at Bamberger Ranch Preserve, Blanco County, Texas. We gathered habitat data from 54 lizards between May 2021 and June 2022, resulting in 859 and 339 points for the macro- and microhabitat analysis, respectively. Macrohabitats used varied by season, with more being occupied during the summer and fall while fewer were occupied during the winter and spring, but resource selection ratios indicated oak/hardwood rocky slope forests were important across all seasons. Microhabitat models indicated *G. infernalis* selects for structural microhabitat (woody plant and debris), rocky refuge, canopy cover, and slope (angle) of hill while avoiding more open areas devoid of structural habitat. In terms of arboreal habitat, *G. infernalis* primarily sought out dense vegetative and woody debris consisting of thin branches and high canopy cover throughout the year. Tree use by *G. infernalis* was random at one site but the other site showed non-random use, with lizards preferring Ashe juniper (*Juniperus ashei*) trees. This use of complex structural habitat provides *G. infernalis* with seasonal needs for foraging, thermoregulating, and avoiding predators. These findings provide new insights into the ecology of this species and will now allow us to compare the ecological traits of Central Texas populations to those occurring in other regions of their distribution.

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Introduction

Understanding broad- and fine-scale habitat characteristics that an animal requires is vital for developing species-specific management plans (Morrison 2001; Miller and Hobbs 2007). Specific habitat needs fluctuate temporally in nature and are often influenced by the availability of resources at different periods (eg seasonal or behavioural periods) that promote survival, such as reproduction, shelter or acquisition of

CONTACT Corey M. Fielder corey.fielder01@tamu.edu

resources (MacArthur and Pianka 1966; Smith and Ballinger 2001). Particularly for ectotherms, temporary environmental features of the habitat (eg temperature, moisture, and light) are important in regulating seasonal activities and use of specific parts of a habitat at both the local and region-specific scale (Heatwole 1977; Munoz and Losos 2018).

Individuals may select locations within vegetation types based on the structural features of their immediate environment (microhabitat); if needed microhabitat characteristics are contained within an exclusive vegetation type then selection of microhabitat should mirror macrohabitat selection (Rasmussen and Litzgus 2010). There are instances, however, where ideal microhabitat exists within a variety of macrohabitats in which selection of microhabitat would be independent (Harvey and Weatherhead 2006; Rasmussen and Litzgus 2010).

Many lizards occupy terrestrial space in mostly two dimensions, but some species exhibit highly arboreal lifestyles, which adds a third, structural dimension to understanding habitat use. For semi-arboreal lizards, many factors such as temperature, seasonality, complexity of microhabitat, predator density, and geography can all affect how lizards use their habitat (Melville and Schulte II 2001; Barreto-Lima *et al*. 2013; Munoz and Losos 2018). Observed differences in activity patterns and movement at different heights within complex arboreal habitats are commonly attributed to strategies for avoiding predators, thermoregulating, and even sleeping (Vitt *et al*. 2002; Singhal *et al*. 2007; Ikeuchi *et al*. 2012; Barreto-Lima *et al*. 2013; Bors *et al*. 2020).

Texas Alligator Lizards (*Gerrhonotus infernalis*) range from Central Mexico and into the southern United States (Powell *et al*. 2016). While it has long been regarded as a single species based on morphological characteristics (Good 1994), recent phylogenetic and phylogenomic research has identified some geographic variation in this lineage that indicates the need for an in-depth study of the taxonomy of this species; despite this, no changes have been made to the species taxonomy (Garcia-Vasquez *et al*. 2018; Blair *et al*. 2022). In Texas, *G. infernalis* occupies rocky hillsides, riparian areas, and wooded canyons stretching throughout the Edwards plateau to the Big Bend region (Greene *et al*. 2009). There are few ecological studies on *G. infernalis*, with only one prior study attempting to quantify their habitat use characteristics in the southern portion of its range near Monterrey, Nuevo Leon, Mexico, which ranges in elevation from 2000 to 4000 ft (Garcia-Bastida 2013). Garcia-Bastida (2013) revealed that *G. infernalis* was primarily terrestrial, inhabited oak and oak–pine forests, and used microhabitat consisting primarily of litter and rocky structures. No arboreal activity was documented for *G. infernalis* by Garcia-Bastida (2013); however, frequent arboreal activity throughout most of the year was recently documented for populations occurring in Central Texas (Fielder *et al*. 2023). It has been documented in widely distributed lizard species that region-specific abiotic and biotic factors (eg topography, habitat availability, community structure) can affect how populations exploit their site-specific habitat (Adolf 1990; Smith and Ballinger 2001; Johnson, Kirby, *et al*. 2006). Thus, it is probable that habitat needs for Central Texas populations differ in comparison to populations occurring in the southern portions of their range as the topography, habitat types, and annual temperatures differ between these two regions.

Our goal was to provide baseline ecological data on habitat use for *G. infernalis* populations occurring in the northernmost extent of their range in Central Texas. Our specific objective for this study was to evaluate seasonal differences in habitat use to include macro- and microhabitat use and arboreal habitat use of *G. infernalis*.

Materials and methods

Study site

Our study was conducted at Selah, Bamberger Ranch Preserve (BRP), a 2225-ha ranch located in Blanco County, Texas, USA, at an elevation of approximately 1200 ft (Figure 1). The landscape consists of hilly terrain, wooded canyons, savannah grasslands, hardwood slope and motte forests, and riparian hardwood and herbaceous areas. We chose two sampling sites on BRP based on preliminary surveys and year-round accessibility 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 two sites are approximately 3 km apart and differ by use, proximity to anthropogenic activities, and vegetation types present. We defined the boundary of these two sites by creating a box that encompassed the extent of all telemetered lizard locations documented in Fielder *et al.* (2023). The THH site is approximately 8.23 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. Ashe juniper (*Juniperus ashei*), Mexican buckeye (*Ungnadia speciosa*), and Texas red oak (*Quercus buckleyi*) represented approximately 78% of the species sampled at THH. RCT is smaller in size (1.33 ha) and consists of a south-facing primarily oak hardwood slope and riparian forest with a small west-to-east-tapering

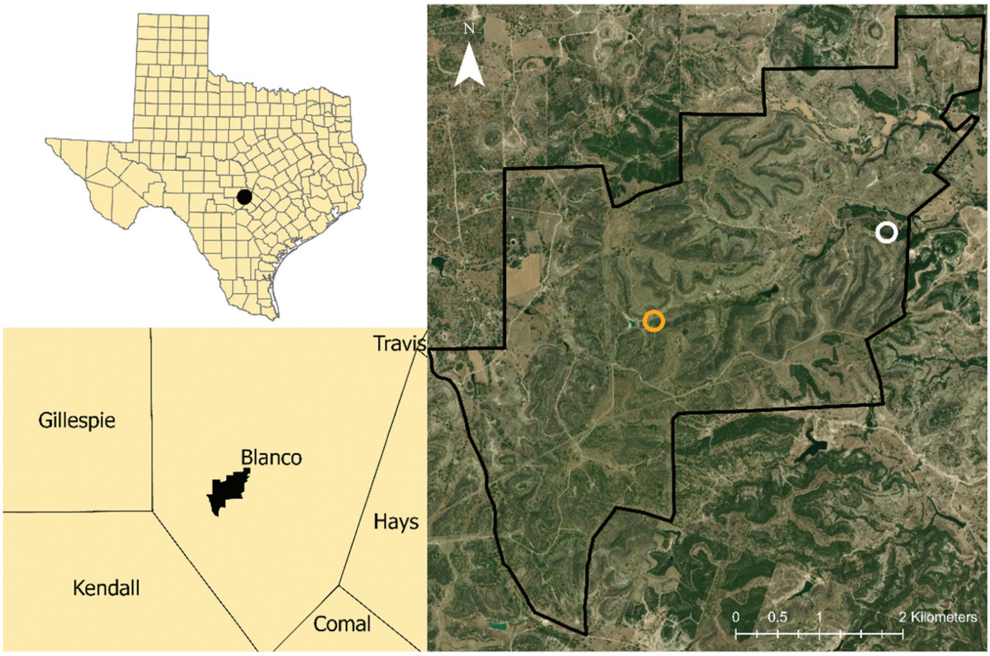

Figure 1. Location of field site at Bamberger Ranch Preserve, Blanco County, Texas. Turkey Hollow Hill (THH) is circled in white, and Rachel Carson Trail (RCT) is circled in orange.

rock wall. Roughleaf dogwood (*Cornus drommondii*), Texas red oak (*Quercus buckleyi*), black cherry (*Prunus serotina*), and possumhaw (*Ilex decidua*) represented approximately 68% of the tree species sampled at RCT. THH is further from anthropogenic activities and not regularly traversed by people, while RCT is more frequently visited and lies directly adjacent to a paved road.

Telemetry procedures

We conducted walking surveys for *G. infernalis* at both THH and RCT between 15 April 2021 and 10 June 2022. Once encountered, we captured *G. infernalis* using the pole and lasso method or by hand. Upon capture, we attached a Model R1635 radio transmitter (Advanced Telemetry Systems Inc. Isanti, Minnesota), or a RECCO tag (RECCO AB. Lidingo, Sweden) if the radio was >7.5% of the individual's body mass (Knapp and Abarca 2009). We attached the radio, or RECCO tag, on the lizard's dorsum approximately 2 cm anterior to the back limbs by applying cyanoacrylate glue and holding in place for 30s. Next, we stimulated the lizard to inflate the abdomen region and used tan micropore surgical tape (3M, St. Paul, Minnesota) to wrap the lizard three times ensuring the tape was flush with the dorsolateral folds as suggested by Garcia-Bastida *et al*. (2012).

We split habitat data seasonally into three-month periods based on the average date of observed behavioural shifts that were documented in Fielder *et al*. (2023): (summer = 10 June–10 September 2021, fall = 10 September–10 December 2021, winter = 10 December–10 March 2022, spring = 10 March–10 June 2022) to determine whether habitat use varied by season. We attempted to track lizards 2–3 days a week during summer, fall, and spring but only one day a week during the winter season as movements were rare, as further described in Fielder *et al*. (2023). To ensure lizards were tracked at different periods of the day, we randomly assigned lizards to groups each week to be located either in the morning (7.00–11.30am), afternoon (1.00–5.30pm), or evening (6.30–10.00pm). For each lizard located, we recorded GPS coordinates, height above ground (m), and any relevant behavioural observations. A Model R410 VHF receiver (Advanced Telemetry Systems Inc. Isanti, Minnesota) or R9 RECCO receiver (RECCO AB. Lidingo, Sweden) was used to determine the lizard's exact position.

Macrohabitat

We defined macrohabitat as habitat comprised of easily discernable physical and biological features (Johnson 1980; Morrison *et al*. 2006). We generally followed the Texas Parks and Wildlife Department's Ecological Mapping System (Elliot *et al*. 2009–2014) guide for delineating broad habitat boundaries unless on-the-ground observations proved different. After tracking a lizard, we assigned them to one of five macrohabitat types: oak/hardwood rocky slope forest (OHRSF), oak/hardwood motte and woodland (OHMW), riparian hardwood/Ashe juniper forest (RHJF), Ashe juniper slope forest (AJSF), or savannah grassland (SG). The OHRSF is characterised by highly sloped terrain, mixed hardwood trees and shrubs, and densely scattered rocky structures, while the OHMW is generally flat and contains fewer rocky structures. The RHJF is densely vegetated with live and fallen dead trees and an ephemeral creek (Miller Creek) running through it, and the AJSF is highly sloped with a mix of rocky structures but is dominated primarily by dense thickets of Ashe juniper. The SG habitat consists of native grasses with scattered tree island clumps spread throughout. During this study, THH consisted of approximately 2.1 ha (26.7%) OHRSF, 1.9 ha (24.7%) OHMW, 0.5 ha (6.4%) RHJF, 0.4 ha (5.7%) AJSF, and 2.9 ha (36.3%) SG. RCT consisted of 0.5 ha (38.8%) OHRSF, 0.1 ha (5.4%) OHWM, 0.3 ha (23.6%) RHJF, and 0.4 ha (32.1%) SG, while no AJSF habitat was present at this site.

We collected macrohabitat data from each telemetered lizard location and then calculated seasonal resource selection functions at the population level using Design II with 95% Bonferroni confidence intervals as suggested in Manley *et al*. (2002). We used the R package adehabitatHS (Calenge 2024) to test for proportional use of habitat by individual lizards (Khi2L1), overall habitat selection (Khi2l2), and whether lizards are on average using vegetation types in proportion to availability, regardless of individual lizard differences (Khi2L2–Khi2L1). We consider selection ratios >1 to signify habitat is used more than available, if the lower confidence interval is above 1 it is considered favoured, and if the upper confidence interval is below 1 it is considered avoided (Manley *et al*. 2002; Jakubas *et al*. 2020). Due to a smaller sample size at RCT (n = 152 locations) in comparison to THH (n = 707 locations) we opted to group the data together for this analysis.

Terrestrial microhabitat

We employed a use and availability approach with a 1:2 ratio sampling design to understand microhabitat use (Manly *et al*. 2002). For each lizard location, we recorded microhabitat variables at the point level (lizard's locations) and frame level (1 m square frame centred on the lizard's location). For each point location we measured the following variables: canopy cover (%, with a spherical densiometer), slope angle of hill (°, using a 0.25 m metal t-bar equipped with a magnetic angle locater), slope aspect of hill (0–359°, with a compass), and distance (m) to nearest rocky structure (>300 mm in diameter) with a measuring tape. For microhabitat variables measured at the frame level, we took a photograph with a Canon Powershot SX60 (Canon Inc. Tokyo, Japan) 1 m above the ground that we used to visually estimate the percent cover of the following variables: woody plant, woody debris, rocky substrate, grass/forbs, leaf litter, bare ground, and rocky structures (>300 mm diameter). We defined woody plants as trees less than 6 m in height, and woody debris was defined as clumps of fallen limbs/sticks that had accumulated on the ground. To compare used and available microhabitat, we paired each used lizard location with two random reference locations measured during the same week if a lizard was >3 m from their previous telemetered location. We used a random number generator to determine distance, between 5 and 30 m (based on average distance travelled between consecutive telemetered lizard locations, X = 7.10, 18.74, 1.70, 7.82 for summer, fall, winter, and spring, respectively), and direction (0–359°) when placing random reference microhabitat points.

We analysed microhabitat data by season (as defined above) with binomial logistic regression using the 'glm' function in the base R stats package to compare used lizard locations with their two paired random reference locations. Logistic regression models are commonly used methods for analysing habitat selection (Drew *et al*. 2010; Nad'o and Kanuch 2018). Although matched pairs logistic regression has grown in popularity for use–availability habitat studies (Keating and Cherry 2004; Emmons 2017), we chose to utilise simple logistic regression with a greater sampling ratio (1:2) as this method has been proven valid for calculating resource selection functions and it is recommended to increase the ratio of use–availability samples for hard-to-detect species (Johnson, Nielsen, *et al*. 2006; Nad'o and Kanuch 2018). We compared used lizard locations (recorded as 1) with their two paired random reference locations (recorded as 0). We initially included all microhabitat variables measured in the models for each season; however, we did not include the variables grass/forb in the winter or spring season analyses as no lizard location contained this variable during those periods. We conducted a Spearman rank-order correlation analysis to test for confounding influences between all combinations of predictor variables and defined strong evidence of correlation as $r > 0.7$. No correlation was greater than $r = 0.49$, therefore, no variables were removed. No single lizard made up a significant percentage of locations per season (median = 12.2%, max = 13.9%), thus reducing likelihood of bias (Row and Blouin-Demers 2006; Sprague 2017).

To determine the best fitting model for each season, we first tested the null model against the additive global model. We assessed the variance inflation factor (VIF) for each variable to identify multicollinearity and removed variables with high VIF if needed. We then used likelihood ratio tests (LRTs) to evaluate the impact of the model's predictive power after removing a variable and then performed univariate logistic regression to test the significance of each predictor variable. Next, we employed the step function with the LRT criterion to suggest a reduced set of candidate variables. Finally, we re-assessed the model using LRT to observe changes in predictive power with the addition or removal of variables to determine our final candidate variables for each season.

Lastly, we created a candidate set of 5–6 models using our final reduced set of candidate variables for each season. To rank candidate models, we used the R package AICcmodavg (Mazerolle 2020) to calculate Akaike's information criterion corrected for small sample size (AICc), the change in AIC values between models (ΔAIC), and Akaike weight (w_i) (Burnham and Anderson 2002). We used the modified criterion because the ratio of sample size (n) to parameters (K) for summer, winter and spring was low (n:K < 40:1); although fall had an acceptable sample size (n:K = 439:10), we still opted to use AICc as both methods tend to select the same model when a sufficiently large sample is used (Burnham and Anderson 2002). We considered models with ΔAICc ≤ 2 highly probable. We then performed model averaging and calculated variable importance for the variables included in the highly probable models ensuring each model contained an equal number of predictor variables using the MuMIn R package (Burnham and Anderson 2002; Barton 2020). We considered variables important predictors of habitat selection if they had a combined model weight ≥0.75 and the 95% confidence intervals around their odds ratio did not include zero.

Arboreal habitat

When *G. infernalis* was arboreal, defined as >1 m above ground, we recorded the following data: canopy cover (%) at the lizard's exact position, perch height above ground (m), slope of hill (°), aspect of hill (0–359°), species of tree, status of tree (dead or live), and diameter at breast height (DBH) of tree trunk. We characterised arboreal perch site by sex and site using descriptive statistics and reported mean ±1 standard error (SE) for each variable.

Next, we sampled woody vegetation using the quadrat method (Gotelli and Colwell 2001) to estimate relative abundance of tree species to understand whether tree preference is occurring or whether use is based on availability. We delineated a sampling polygon at each site using the ArcGIS Desktop 2.7.3 (Environmental Systems Research Institute, 2021) to encompass only the area where lizards in an arboreal state were tracked. We then used the geoprocessing tool 'create random points' to randomly place 10 × 15 m quadrats in each section, ensuring at least 20% of each site was sampled. We sampled 37 quadrats (5,600 m^2) at THH and 12 quadrats (1800 m^2) at RCT, equalling 20.1 and 28.3% of each section sampled, respectively. For each sampling quadrat, we counted individual woody plant species (>1 m in height) and then calculated the average number of woody plant species per quadrat. We then calculated the Simpson's index of diversity (SID; 1–*D*) for each site and with combined site data (Morris *et al*. 2014). Due to a smaller sample size of arboreal points at RCT (n = 29) in comparison to THH (n = 211), we calculated chi square tests of independence by site and with grouped data to determine whether tree use is different from what would be expected under random use.

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) and ArcGIS Desktop 2.7.3 (Environmental Systems Research Institute, 2021). We reported all means ± 1 SE, and all statistical tests were considered significant at $\alpha = 0.05$.

Results

We captured 54 *G. infernalis*, 27 males (mean snout-vent length (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) between 15 April 2021 and 15 May 2022. We did not include 7 individuals in the habitat analysis (n= 2 males, 2 females, 3 juveniles) because they were captured at different sites during preliminary surveys or were too small to safely attach radios or RECCO tags. In total, we obtained data from 927 recorded lizard locations (mean per lizard = 18.6 locations, range 1–64 locations). Time of attachment varied between radios (mean = 30.9 days, range 7–82 days) and RECCO tags (mean = 94.0 days, range 7–219 days). The radio transmitters and RECCO tags did not appear to hinder *G. infernalis* movements as we observed them exhibiting natural behaviours when compared to non-telemetered lizards. For example, radioed *G. infernalis* were observed climbing arboreally, inhabiting rocky refugia and feeding, and a radioed pair were observed copulating. However, this could have altered habitat use in some form. For example, radios could have prevented lizards from getting as deep into rocky crevices as their counterparts, but all lizards tracked through the winter season survived, indicating they were still able to successfully find suitable rocky refugia. Based on this, we believe our procedures did not significantly alter this species' ability to find resources during this study, which thus gives us some degree of confidence in our results.

Table 1. Proportions of available and used vegetation types, selection ratios (Wi), standard error (SE), and 95% Bonferroni corrected confidence intervals for resource selection functions describing seasonal macrohabitat use of Texas Alligator Lizards (*Gerrhonotus infernalis*) at Bamberger Ranch Preserve, Blanco County, Texas.

Season	Vegetation type	Available	Used	Wi	SE	95% CI
Summer	OHRSF	0.28	0.67	2.37	0.44	1.24, 3.49
	OHMW	0.22	0.22	1.01	0.60	−0.53, 2.56
	RHJF	0.09	0.11	1.19	0.70	−0.62, 2.98
	OAJS	0.05	0.00	0.00	0.00	0.00, 0.00
	SG	0.36	0.00	0.00	0.00	0.00, 0.00
Khi2L1	258.74, $df = 68$, $p = 0.001$					
Khi2L2	521.34, $df = 72$, $p = 0.001$					
Fall	OHRSF	0.28	0.54	1.92	0.24	1.30, 2.54
	OHMW	0.22	0.24	1.09	0.24	0.46, 1.72
	RHJF	0.09	0.06	0.63	0.33	−0.21, 1.48
	OAJS	0.05	0.02	0.42	0.36	−0.52, 1.35
	SG	0.36	0.14	0.39	0.09	0.15, 0.62
Khi2L1	390.67, $df = 116$, $p = 0.001$					
Khi2L2	525.83, $df = 120$, $p = 0.001$					
Winter	OHRSF	0.28	0.80	2.83	0.42	1.74, 3.92
	OHMW	0.22	0.11	0.51	0.45	−0.65, 1.68
	RHJF	0.09	0.00	0.00	0.00	0.00, 0.00
	OAJS	0.05	0.08	1.68	1.65	−2.57, 5.93
	SG	0.36	0.00	0.00	0.00	0.00, 0.00
Khi2L1	152.02, $df = 68$, $p < 0.050$					
Khi2L2	364.21, $df = 72$, $p = 0.001$					
Spring	OHRSF	0.28	0.73	2.56	0.28	1.83, 3.29
	OHMW	0.22	0.17	0.79	0.31	−0.01, 1.59
	RHJF	0.09	0.04	0.42	0.42	−0.67, 1.51
	OAJS	0.05	0.06	1.25	1.03	−1.41, 3.91
	SG	0.36	0.00	0.00	0.00	0.00, 0.00
Khi2L1	177.28, $df = 68$, $p < 0.050$					
Khi2L2	378.29, $df = 72$, $p = 0.001$					

Macrohabitat abbreviations are as follows: OHRSF = oak/hardwood rocky slope forest, OHMH = oak/hardwood motte and woodland, RHJF = riparian hardwood/Ashe juniper forest, AJSF = Ashe juniper slope forest, OAJS = Oak/Ashe juniper slope SG = savannah grassland.

Macrohabitat

We collected macrohabitat data from 707 locations at THH from 19 males and 16 females, and 152 locations at RCT from 6 males and 6 females. No single lizard made up a significant percentage of locations per season at THH (median = 6.1%, max = 17.3%). As indicated, there were fewer lizards tracked per season at RCT which consisted of summer ($n = 2$, median = 50%, max = 53.3%), fall ($n = 6$, median = 16.6%, max = 35.1%), winter ($n = 4$, median = 23.7%, max = 47.4%) and spring ($n = 3$, median = 34%, max = 38.5%).

The analyses indicated lizards were using macrohabitat types disproportionally to their availability during each season (Khi2L2–Khi2L1, all seasons $p < 0.001$). The resource selection ratios indicated positive selection ratios for OHRSF across all seasons (Wi = 2.37, 1.92, 2.83, 2.56 for summer, fall, winter and spring, respectively) compared to random use or avoidance of the other vegetation types available (Table 1). Vegetation types occupied increased or decreased within seasons, with the fall breeding season containing the highest number of vegetation types used ($n = 5$) and winter season being the lowest ($n = 3$).

Table 2. Combined Turkey Hollow Hill and Rachel Carson Trail descriptive statistics for seasonal microhabitat use for Texas Alligator Lizards (*Gerrhonotus infernalis*) at Bamberger Ranch Preserve, Blanco County, Texas.

	Summer 2021		Fall 2021		Winter 2021/22		Spring 2022	
Variable	Used (*n*= 89)	Reference (*n*= 177)	Used (*n*= 147)	Reference (*n*= 292)	Used (*n*= 36)	Reference (*n*= 72)	Used (*n*= 67)	Reference (*n*= 133)
Canopy cover (CC)	95.5 ± 0.72	85.5 ± 1.47	80.5 ± 2.45	69.3 ± 2.26	93.6 ± 2.77	84.7 ± 0.42	94.7 ± 0.90	85.6 ± 2.07
Slope (SL)	18.3 ± 1.18	13.1 ± 0.70	13.1 ± 1.02	10.3 ± 0.53	23.7 ± 2.26	14.4 ± 1.04	20.3 ± 1.83	14.1 ± 0.86
Dist. rocky refuge (DRF)	2.8 ± 0.51	4.9 ± 0.43	9.4 ± 0.99	8.9 ± 0.63	0.7 ± 0.64	3.9 ± 0.57	1.7 ± 0.32	4.8 ± 0.43
Woody plant (WP)	27.6 ± 2.53	7.9 ± 0.92	26.1 ± 0.23	7.2 ± 0.78	12.1 ± 3.62	9.5 ± 1.53	23.9 ± 2.89	9.1 ± 1.42
Rocky substrate (RS)	3.5 ± 0.90	8.7 ± 0.79	2.7 ± 0.60	8.1 ± 0.75	4.7 ± 0.93	10.9 ± 1.29	5.1 ± 0.70	9.5 ± 0.98
Woody debris (WD)	34.6 ± 2.77	19.8 ± 1.05	30.6 ± 2.02	13.4 ± 0.92	12.9 ± 3.44	17.4 ± 1.64	27.6 ± 3.20	12.7 ± 1.08
Rocky refuge (RF)	12.8 ± 2.53	8.1 ± 1.14	12.1 ± 2.13	4.4 ± 0.70	58.6 ± 6.00	6.1 ± 1.71	26.7 ± 3.55	6.7 ± 1.48
Grass/forbs (GF)	1.6 ± 0.88	9.4 ± 1.60	10.5 ± 1.75	29.1 ± 2.01	0	9.7 ± 2.48	0	12.9 ± 2.22
Leaf litter (LL)	11.8 ± 1.14	25.9 ± 1.52	16.2 ± 1.36	29.4 ± 1.51	8.1 ± 1.70	35.1 ± 2.68	13.5 ± 1.58	26.1 ± 1.91
Bare ground (BG)	2.8 ± 0.84	14.0 ± 1.46	1.7 ± 0.50	7.6 ± 0.85	3.3 ± 1.10	7.9 ± 1.60	2.6 ± 0.65	22.1 ± 0.03

Units are reported as mean ± SE.

Terrestrial microhabitat

We collected microhabitat data on 339 unique used locations (*n* = 280 THH, 59 RCT) and 674 random reference locations between the two sites (Table 2). Locations that qualified for inclusion in the analyses consisted of 89 (mean per lizard = 5.2, range 1–11), 147 (mean = 5.3, range 1–18), 36 (mean = 2.1, range 1–5), and 67 (mean = 3.0, range 1–7) for the summer, fall, winter, and spring seasons, respectively. No single lizard made up a significant percentage of locations per season (median = 12.2%, max = 13.9%). For model selection, bare ground and leaf litter were removed during variable reduction for all seasons as they did not contribute significantly to differences between used and random reference locations. Woody plant, woody debris, and rocky refuge (hereafter described as the primary covariates) were included in the top-ranked models, and model averaging indicated they were consistently important predictors of lizard microhabitat use across seasons (Tables 3 and 4).

Lizards were found at locations with greater canopy cover, slope, woody plant, woody debris, and rocky refuge compared to the random reference locations during the summer season (Table 2). Model averaging indicated the primary covariates and canopy cover were important predictors of site use (Tables 3 and 4). During the fall breeding season, lizards began spreading out away from the more commonly used OHRSF resulting in a greater concentration of locations with grass/forbs during this period. There was again

Table 3. Top six logistic regression models for each season used to evaluate microhabitat use for Texas Alligator Lizards (*Gerrhonotus infernalis*) at Bamberger Ranch Preserve, Blanco County, Texas.

Model	K	AICc	Delta AICc (Δ*i*)	AICc Wt (*wi*)	LL
Summer					
WP + WD + RR + CC + RS	6	163.58	0	0.64	−75.63
WP + WD + RR + CC	5	164.76	1.18	0.36	−77.26
WP + WD + RR + RS	5	177.77	14.2	0	−83.77
WP + WD + CC + RS	5	215.56	51.98	0	−102.66
WP + RR + CC + RS	5	241.51	77.94	0	−115.64
WD + RR + CC + RS	5	251.16	87.59	0	−120.47
Fall					
WP + WD + RR + GF + SL	6	339.87	0	0.68	−163.84
WP + WD + RR + GF	5	341.46	1.59	0.31	−165.66
WP + WD + RR + SL	5	349.12	9.24	0.01	−169.49
WP + WD + GF + SL	5	406.33	66.46	0	−198.1
WP + RR + GF + SL	5	448.84	108.96	0	−219.35
WD + RR + GF + SL	5	462.04	122.16	0	−225.95
Winter					
RR + WP + WD + SL	5	51.76	0	0.75	−20.58
RR + WP + WD	4	54.11	2.35	0.23	−22.86
RR + WP + SL	4	59.37	7.61	0.02	−25.49
RR + WD + SL	4	69.69	17.93	0	−30.65
WP + WD + SL	4	124.59	72.84	0	−58.1
Spring					
WD + RR + WP + CC + DRF	6	112.14	0	0.63	−48.78
WD + RR + WP + CC	5	115.2	3.06	0.14	−51.38
WD + RR + WP + DRF	5	115.23	3.09	0.13	−51.4
WD + WP + CC + DRF	5	115.85	3.71	0.1	−51.71
WD + RR + CC + DRF	5	155.17	43.04	0	−71.37
RR + WP + CC + DRF	5	175.72	63.58	0	−81.64

K = number of parameters, AICc = Akaike's information criterion corrected for small sample size, Δi = AIC differences from the top ranked model, wi = Akaike weights, LL = log likelihood, WD = woody plant, WP = woody plant, RR = rocky refuge, CC = canopy cover, RS = rocky substrate, GF = grass/forbs, SL = slope, DRF = distance to rocky refuge.

Table 4. Coefficients, standard error (SE), odds ratios, confidence intervals (CI), variable importance, and associated *p* values for model averaged covariates used in candidate models to describe seasonal microhabitat use of Texas Alligator Lizards (*Gerrhonotus infernalis*) at Bamberger Ranch Preserve, Blanco County, Texas.

Variable	Coefficient	SE	Odds ratio	95% CI	Importance	*p* value
Summer						
WD	0.11	0.02	1.13	0.08, 0.15	1	<0.001
WP	0.11	0.02	1.13	0.08, 0.15	1	<0.001
RR	0.09	0.02	1.09	0.06, 0.12	1	<0.001
CC	0.10	0.03	1.10	0.04, 0.15	1	<0.001
RS	0.05	0.03	1.05	0.00, 0.10	0.64	0.043
Fall						
WD	0.07	0.01	1.08	0.06, 0.09	1	<0.001
WP	0.08	0.01	1.09	0.06, 0.10	1	<0.001
RR	0.07	0.01	1.07	0.05, 0.09	1	<0.001
GF	0.02	0.01	1.03	0.01, 0.04	0.99	< 0.001
SL	0.03	0.02	1.03	0.00, 0.06	0.69	0.060
Winter						
RR	0.13	0.03	1.14	0.07, 0.19	1	<0.001
WP	0.10	0.03	1.11	0.04, 0.15	1	<0.001
WD	0.09	0.04	1.09	0.02, 0.17	0.98	0.015
SL	0.11	0.06	1.11	0.00, 0.22	0.77	0.049
Spring						
WD	0.13	0.02	1.14	0.08, 0.17	1	<0.001
WP	0.09	0.02	1.09	0.05, 0.12	1	<0.001
RR	0.09	0.02	1.09	0.06, 0.12	1	<0.001
CC	0.08	0.03	1.08	0.01, 0.14	0.92	0.016
DRF	−0.25	0.13	0.78	−0.50, 0.01	0.77	0.052

Macrohabitat abbreviations are as follows: OHRSF = oak/hardwood rocky slope forest, OHMH = oak/hardwood motte and woodland, RHJF = riparian hardwood/Ashe juniper forest, AJSF = Ashe juniper slope forest, SG = savannah grassland. Microhabitat variable abbreviations are as follows: WD = woody debris, WP = woody plant, RR = rocky refuge, CC = canopy cover, RS = rocky substrate, GF = grass/forbs, SL = slope, and DRF = distance to rocky refuge.

higher canopy cover, woody plant, woody debris, and rocky refuge compared to random reference locations, but model averaging indicated the primary covariates along with grass/forbs were important predictors of fall microhabitat use.

During the winter season, we saw a shift to locations with higher percentages of slope and rocky refuge (Table 2). Model averaging indicated the primary covariates were important predictors of winter microhabitat use along with slope to a lesser extent (Tables 3 and 4). For the spring season, we saw similar results to summer with greater canopy cover, slope, woody plant, woody debris, and rocky refuge percentages in used locations. Model averaging identified the primary covariates along with canopy cover, and to a lesser extent distance rocky to refuge, as important predictors of spring microhabitat.

The mean aspect for all seasons was primarily north for used and random reference locations at THH as this entire site is generally north facing. At RCT, lizards were commonly found on any slope during spring, summer and fall; however, during winter all tracked lizards overwintered in the south-facing rock wall.

Arboreal habitat

We collected arboreal habitat data on 240 unique locations (THH = 211, RCT = 29) between 1 June 2021 and 3 June 2022. Due to some *G. infernalis* perching in an arboreal

Table 5. Descriptive statistics of arboreal microhabitat use Turkey Hollow Hill (THH) and Rachel Carson Trail (RCT) for Texas Alligator Lizards (*Gerrhonotus infernalis*) at Bamberger Ranch Preserve, Blanco County, Texas.

Site	Canopy cover	Ground slope	DBH (cm)	Branch diameter (cm)	Live/dead
THH (*n* = 211 locations)	95.8 ± 0.45	17.1 ± 0.69	12.5 ± 0.60	3.4 ± 0.34	155/55
RCT (*n* = 29 locations)	95.3 ± 1.15	16.0 ± 2.95	7.6 ± 1.50	2.8 ± 0.87	24/5

Units are reported as mean ± standard error (SE). DBH = diameter at breast height, and live/dead refers to the trees measured.

location that was higher than we could reach (>2.5 m in height), or on a fallen dead limb suspended within the canopy of a second tree, we were only able to record 202 and 238 measurements for branch diameter and DBH, respectively. There were no differences observed in arboreal microhabitat use by sex (n = 154 M, 86 F) for canopy cover ($W = 6948.5$, $p = 0.524$), ground slope ($W = 6773.5$, $p = 0.770$), DBH ($W = 6517.5$, $p = 0.972$), or branch diameter ($W = 4472$, $p = 0.730$); therefore, sexes were grouped together by site (Table 5). Lizards at both sites were primarily found on thin branches extending from the main trunks of densely clumped smaller diameter trees under high canopy cover and on sloped terrain.

At THH, we sampled 779 trees representing 18 species, giving a SID of 0.650, with Ashe juniper representing 56.6% (n = 441) of the tree species. Tree use by *G. infernalis* at THH consisted of 71.4% (n= 142) Ashe juniper trees followed by Texas red oak (*Quercus buckleyi*) at 12.6%. At RCT, we sampled 274 trees representing 19 species, giving an SID of 0.836, with roughleaf dogwood (*Cornus drommondii*) representing 33.5% (n = 92) of the tree species. Tree use by *G. infernalis* at RCT consisted of 20.7% (n = 6) Texas red oak followed by roughleaf dogwood at 13.8%. At THH, the observed distribution of trees used was lower than what would be expected if random use was occurring ($x^2 = 61.424$, $df = 17$, $p < 0.001$), but no association between used trees and sampled available trees was evident at RCT ($x^2 = 22.934$, $df = 19$ $p = 0.240$). The combined tree availability and use across both sampling sites resulted in an SID of 0.786 and the distribution of trees used was lower than what would be expected if random use was occurring ($x^2 = 62.301$, $df = 23$, $p < 0.001$).

Discussion

Macrohabitat

Gerrhonotus infernalis occupied more macrohabitat types during the summer and fall, and fewer in the winter and spring seasons. As documented in Fielder *et al*. (2023), the fall breeding season includes the highest movement rates and space occupied by *G. infernalis* during the year with the least during the winter and early spring (when lizards are overwintering and emerging) in Central Texas. Similar findings were documented in Garcia-Bastida (2013) with the highest number of captures and habitat types used by *G. infernalis* occurring in the fall (autumn) breeding season, with the least during the winter and spring near Monterrey, Nuevo Leon, Mexico.

Gerrhonotus infernalis primarily selected for OHRSF across all seasons. The adjacent vegetation types, RHJF, OHMW, and OAJS, had > 1 selection ratios for summer, fall, and winter, respectively, but were considered randomly used based on 95% confidence intervals. Similar observations were documented in Garcia-Bastida (2013) but with oak forests being primarily used across years with seasonal variation in the adjacent oak–pine and pine–oak forests. It has been documented that animals often have different habitat requirements for different seasonal activities (eg mating, reproduction, and other resource needs); therefore, animals may occupy different habitat types at different periods (Rutherford and Gregory 2003). However, some habitats offer all needed resources and thus the need for seasonal long-distance movements is not necessary (Rutherford and Gregory 2003). The high selection ratios for OHRSF across all seasons indicates this habitat provides much of the needed resources (ie rocky structures and structural habitat) for thermoregulation, reproduction, feeding and overwintering activities by *G. infernalis* in Central Texas.

Terrestrial microhabitat

Gerrhonotus infernalis exhibited slight variation in microhabitat use by season, but largely selected for sites with higher percentages of woody plant and debris (structural microhabitat) and rocky structures across all seasons while avoiding more open sites consisting chiefly of leaf litter, bare ground, rocky substrate, or grass/forbs. Canopy cover and slope of hill varied by season in response to resource needs; canopy cover was more important during the warmer seasons for thermoregulating while slope was more important during the winter as their overwinter sites (rocky structures) were mainly located on hillsides. Structural habitat and rocky structures can provide *G. infernalis* with varying thermal microclimates, predator avoidance and foraging opportunities (Melville and Shulte II 2001; Bentz *et al*. 2011; Bors *et al*. 2020).

This selection of rocky crevices and avoidance of open areas devoid of such structures by *G. infernalis* is a common trait documented in many ectotherms, as deep rock crevices can provide more stable thermal environments during winter as well as egg laying sites for *G. infernalis* in the spring (Ibarguengotyia *et al*. 2008; Greene *et al*. 2009; Bentz *et al*. 2011). A notable aspect of winter habitat use was the sharing of rock crevices among many *G. infernalis*, which we observed on four occasions. Measuring environmental characteristics within rock crevices was out of the scope of this present study, but this aggregating behaviour could indicate that suitable rock crevices are a limiting resource at these sites, sharing is more beneficial for thermoregulatory purposes, or perhaps some form of kin aggregation may be occurring as documented in other reptile species (Vitt 1974; Shah *et al*. 2003; Bishop and Echternacht 2004; Gardner *et al*. 2016).

The grass/forbs variable was considered an important predictor of fall microhabitat use for *G. infernalis*, which coincides with the increased movements and habitat types occupied during the fall breeding season (Fielder *et al*. 2023). When *G. infernalis* was tracked in the savannah grassland during the day, we observed them within the tall grass or tree island clumps, but *G. infernalis* was only found perched in the tree island clumps when tracked during the evening or night. This suggests that grass/forbs are not essential to *G. infernalis* per se, but instead represent more of a transitional microhabitat they are passing through while in search of mates or moving among tree island refuges. These results indicate that *G. infernalis* is selecting microhabitat independently of macrohabitats as the same variables (ie canopy cover, woody plant, and woody debris) were used within all macrohabitat types.

Different findings were documented in Garcia-Bastida (2013) in which *G. infernalis* was primarily associated with high concentrations of leaf litter during the summer and fall but similar in winter and spring with high concentrations of rock or rock wall near Monterrey, Nuevo Leon, Mexico. This could be a consequence of bias in locations documented in Garcia-Bastida (2013) as surveys were conducted only along trails and footpaths within the study area, but it could also be due to thermal needs and what is available for *G. infernalis* between these two regions. It has been documented in lizard species inhabiting different elevational gradients that microhabitats that are otherwise suitable can be thermally insufficient depending on local thermal environments (Adolph 1990). Leaf litter may provide adequate thermal refugia and foraging opportunities in the higher elevational regions of Nuevo Leon, Mexico, whereas arboreal activity may be more effective for thermoregulating and foraging in the more extreme temperatures of Central Texas. There is a need to investigate the thermal characteristics found within used sites to better clarify whether this is an important factor in microhabitat use here. Additionally, future studies on *G. infernalis* habitat use should focus on longer periods as well as obtaining larger sample sizes to better understand whether these trends hold true across varying climatic years (ie wetter versus drier years).

Arboreal habitat

Gerrhonotus infernalis exhibited similar arboreal microhabitat use characteristics at both THH and RCT, with individuals primarily perching under dense canopy cover on thin horizontal branches of dense shrub tree clumps, tree falls (eg small fallen trees overhanging rock edges) and woody debris piles. It has been documented in other arboreal and semi-arboreal lizard species that the use of dense vegetative structures, narrow and unstable branches, and even head perch direction are factors in reducing the risk of predation (Mohanty *et al*. 2016; Bors *et al*. 2020). *Gerrhonotus infernalis* is cryptic due to its colouration and elongated morphology; thus, this arboreal use of complex structural habitat likely aids in not only predator evasion but also thermoregulation, sleep and foraging activities (Melville and Shulte II 2001; Ralidis and Acunas 2012; Bors *et al*. 2020).

Gerrhonotus infernalis appears to be using tree species randomly at RCT, but the analysis indicated non-random use of trees at THH as well as non-random use of trees with combined data from both sites. The main differences between these two sites were that fewer individual lizards were captured and tracked at RCT (n = 12) in comparison to THH (n = 35), leading to fewer arboreal points being collected at RCT. The second difference was that Ashe juniper was highly abundant and the most used tree species at THH while relatively few Ashe junipers were found in the RCT study site. Previous field observations, particularly within the Barton Creek greenbelt area of Austin, Texas, found few *G. infernalis* inhabiting Ashe juniper (or generally cedar) trees, which was thought to be a result of the oils and resins being noxious to them (Ralidis and Acuna 2012). Our observations indicate the dense Ashe juniper clumps present at THH appear to provide ample opportunities for *G. infernalis* to traverse varying microthermal climates, forage and sleep while remaining highly concealed during the warmer months. The differences between these two areas may simply be a product of where the concentrated observations of this species are occurring at Barton Creek (eg only along trails or in rocky areas devoid of cedar trees). A more thorough study of the Barton Creek *G. infernalis* populations is needed for comparison and to better clarify the arboreal tendencies and apparent preference for Ashe juniper trees observed at our site in relation to what is available.

Although frequent arboreal habitat use was observed in this study, it was not documented in Garcia-Bastida (2013). Regional variation (ie geography and thermal regimes) across a species' range can influence differing life history traits such as growth, thermal preferences and performance of lizards (Garland and Adolph 1991; Miles 1994; Smith and Ballinger 2001). For example, variation in arboreal habitat use as a function of geography has been documented in *Anolis* and *Sceloporus* lizards in North America (Adolph 1990; Munoz and Losos 2018). Low-elevation populations for both species tended to perch on arboreal vegetation while high-elevation populations were more terrestrial and used rocky substrate which was considered an adaptive strategy to conform to region-specific thermal variation (Adolph 1990; Munoz and Losos 2018). *Gerrhonotus infernalis* can tolerate a wide range of temperatures and is considered a thermoconformer (Garcia-Bastida 2013; Lazcano *et al.* 2022). Therefore, the arboreal tendencies seen in Central Texas populations are potentially an adaptive strategy to maintain optimal body temperatures in a region that experiences more extreme thermal variations across a year.

Conclusions and recommendations

Our results indicate that Central Texas populations of *G. infernalis* are strongly associated with structural habitat in terms of woody plant and debris, and rocky refuge which is commonly found on mixed hardwood rocky slope forests throughout the region, while canopy cover and slope of hill vary by seasonal needs. Although it was previously thought that *G. infernalis* avoided Ashe juniper trees, it is apparent that this tree is preferred when present in suitable macrohabitat but not needed to sustain arboreal activities. Clear-cutting and removal or thinning of mid- and understory vegetation would remove needed structural habitat that this species relies on, and the elimination of rocky complexes where shelter, brooding and reproduction occur could negatively impact the persistence of *G. infernalis* populations.

Although this study provides insights into Central Texas populations, it is evident that the results presented here do not apply to populations occurring in other regions across this species range. Populations of *G. infernalis* occurring near Monterrey, Nuevo Leon, Mexico, inhabited oak–pine forests and primarily used leaf litter and rocky structures, whereas Central Texas populations selected largely for structural (arboreal habitat) and rocky structures. It is probable that these variations are due to the elevation and thermal gradients found between these two regions (Blanco County, Texas ~1200 ft, and Monterrey ~2000–4000 ft) which may require different thermoregulation strategies. The same can likely be said, for example, of the Big Bend region of Texas (ranging from 4000–7800 ft of elevation) which contains high densities of *G. infernalis*, but more studies on the thermal ecology of this species are needed to support this reasoning. Thus, there is a need for additional studies across this species' range comparing how their behaviour and resource procurement strategies are adapted to the topography and climatic differences between regions.

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ORCID

Corey M. Fielder http://orcid.org/0000-0003-3043-2608
Wade A. Ryberg http://orcid.org/0000-0003-2548-8113
Danielle K. Walkup http://orcid.org/0000-0001-6836-4212
Jared M. Holmes http://orcid.org/0009-0004-9942-5726
Toby J. Hibbitts http://orcid.org/0000-0001-7126-6891

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