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DIURNAL AND NOCTURNAL HABITAT USE IN RETICULATE COLLARED LIZARDS (*CROTAPHYTUS RETICULATUS*)

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ABSTRACT—Patterns of habitat use in animals can vary over time and space in predictable ways. For ectotherms, behavioral cycles are tightly linked to varying temperatures in the environment such that microhabitat availability can constrain individual performance, fitness, and life history. A long history of research on diurnal microhabitat use in lizards exists; however, comparatively little is known about nocturnal microhabitat use that might also constrain individual lizard performance, fitness, and life history. In this study, we compared diurnal and nocturnal microhabitat sites of the reticulate collared lizard (*Crotaphytus reticulatus*), a threatened species in Texas, to available microhabitat sites. We found significant differences between diurnal and nocturnal microhabitat characteristics, and both of these were significantly different from random microhabitat sites available. We observed that *C. reticulatus* used diurnal and nocturnal microhabitats with a gravel substrate and scattered boulders that were covered by a short overstory of woody and succulent plants rather than more heavily vegetated sites with dense grasses and forbs. We also observed that diurnal microhabitats were moderately open, shallow gravel slopes compared with nocturnal microhabitats that contained dense thickets of woody and succulent plants. The open, gravelly characteristics of diurnal microhabitats with occasional vegetative structure were more consistent with microhabitat descriptions of other Crotaphytids, which as a group are visual predators. However, the daily shift to dense, thorny plant cover at night appears unique to *C. reticulatus* among Crotaphytids in general. This study suggests that private land stewardship across the *C. reticulatus* distribution in Texas has benefitted the species by maintaining habitat used by the lizard, and it suggests that future conservation actions for the species will be most successful with continued engagement with private landowners.

RESUMEN—Patrones en el uso del hábitat por animales varían en el tiempo y el espacio de manera predecible. Para los ectotermos cuyos ciclos de comportamiento se relacionan estrictamente con la variación de temperaturas en el medio ambiente, la disponibilidad de microhábitats puede limitar la capacidad física individual, la adecuación y la historia de vida. Aunque existe amplia investigación sobre el uso del microhábitat diurno por las lagartijas, se conoce poco sobre el uso de sus microhábitats nocturnos, los cuales también podrían impactar su capacidad física individual, adecuación e historia de vida. En este estudio, comparamos sitios de microhábitats diurnos y nocturnos de lagartijas de collar reticulada del noreste (*Crotaphytus reticulatus*), una especie amenazada en Texas, con sitios de microhábitats disponibles. Encontramos diferencias significativas entre las características del microhábitat diurno y nocturno, y ambas fueron significativamente diferentes a los sitios aleatorios de microhábitats disponibles. Observamos que *C. reticulatus* utilizaba microhábitats diurnos y nocturnos con sustrato de grava y rocas dispersas cubiertas con un dosel vegetal bajo compuesto de arbustos y plantas suculentas, en lugar de sitios tupidos de vegetación con hierbas y herbáceas densas. También observamos que los microhábitats diurnos eran moderadamente abiertos, de grava y no empinados en comparación con los microhábitats nocturnos, que contenían matorrales densos de plantas leñosas y suculentas. Las características abiertas y gravosas de los microhábitats diurnos con estructura de vegetación ocasional son más consistentes con descripciones de microhábitats de otros crotafítidos, que como grupo son depredadores visuales. Sin embargo, el cambio diario a cobertura de plantas espinosas y densas durante la noche parece ser único para *C. reticulatus* entre los crotafítidos en general. Este estudio sugiere que las prácticas de manejo en las tierras privadas de Texas han beneficiado a la especie al mantener el hábitat utilizado por *C. reticulatus* a través de su distribución y sugiere que esfuerzos futuros de conservación de la especie tendrán más éxito si se involucra de manera continua a los propietarios privados.

An organism's habitat encompasses the set of physical environmental factors required for its survival and reproduction (Block and Brennan, 1993). These environmental factors shift continuously over time and vary across the landscape causing organisms to behaviorally adjust to ever changing conditions through a process called habitat selection (Hutto, 1985). The actual distribution of individuals across habitat types, or the observed pattern of habitat use, is a result of the habitat selection process (Hutto, 1985; Block and Brennan, 1993). Patterns of habitat use for organisms can vary over time and space in predictable ways (Stamps, 2009). Temporally, organisms may require different seasonal habitats for specific activities such as reproduction or long periods of inactivity such as hibernation or estivation (Stamps, 2009). Spatially, organisms may forage within several different habitats throughout the day, or across seasons and years (Heatwole and Taylor, 1987).

For ectotherms, ephemeral physical features of habitat such as temperature, moisture, and light are important in controlling the timing of daily and seasonal activities and use of particular parts of the habitat (Heatwole, 1977). These features of the habitat can change rapidly, but structural attributes such as the geometric configuration of the habitat (Ryberg et al., 2015), surface slope and aspect (Hibbitts et al., 2013), presence or absence of crevices, substrate texture, and density of overhead canopy can serve to minimize their fluctuations (e.g., Bartlett and Gates, 1967; Pearson, 1977; Bakken, 1989; Bashey and Dunham, 1997). For example, different substances in the environment absorb, conduct, and lose heat at different rates depending on surface reflectivity, slope and aspect, and the presence or absence of shade. This creates a microdistribution of thermal habitats that contain many temperature gradients (Heatwole, 1977). These microhabitats provide different biophysical environments that can facilitate or constrain ectotherm activity and modify their growth rates, reproduction, and survivorship (i.e., their life histories; see Dunham et al., 1989).

Researchers have a long history of using lizards to study microhabitat use (reviewed in Heatwole, 1977; Smith and Ballinger, 2001) because their diurnal behavior cycle is tightly linked to the varying temperatures of microhabitat patches (Gans and Pough, 1982). Lizards often choose microhabitats with solar radiation and warm surfaces to maintain their body temperatures within an optimal range (Heatwole and Taylor, 1987). However, these sources of heat are not available at night, and the lizard's body temperature gradually drops to that of the surrounding air. Some lizards may seek refuge in burrows, where they will be safe from predators until dawn and the early morning warm-up period (Heatwole, 1977). Unfortunately, we know comparatively little about nocturnal microhabitat use in lizards and even less about its effects on individual performance, fitness, and life history.

Within the genus *Crotaphytus,* collared lizards follow a general pattern of activity that begins with early morning basking, followed by prey-searching, intensive sunning activity, retreat during extreme temperatures, reemergence for afternoon basking, limited foraging until dusk, and then retreat to nocturnal refuge (Fitch, 1956; Montanucci, 1971; McGuire, 1996). For all but one species within the genus, this pattern of diurnal activity takes place within rocky outcrops where microhabitat characteristics such as rock morphology, rock height, number of crevices, and amount of rock cover are commonly found to be important aspects of diurnal microhabitat use (Ruby, 1986; McGuire, 1996). These rocky habitats are also thought to provide nocturnal refuges for collared lizards (Fitch, 1956), but no formal study of nocturnal habitat use has been conducted within the group.

In contrast, the reticulate collared lizard (*Crotaphytus reticulatus*) occupies rolling terrain containing shallow, gravelly soils interspersed with flatlands consisting of clay soils and sandy loam accumulations where large rock outcrops generally are not present (Montanucci, 1971, 1976). For this species, the same general *Crotaphytus* pattern of activity occurs within desert thornscrub habitat characteristic of the Tamaulipan biotic province of southern Texas and adjacent Mexico (Fig. 1; Montanucci, 1971, 1976; Husak and Ackland, 2003). Shrub cover and *Opuntia* thickets vary from moderately open to dense, creating a maze of light and dark shadows where sunlight filters through the branches and *Opuntia* pads (Montanucci, 1971, 1976). Within this habitat, *C. reticulatus* has been observed shuttling between understory light and dark patches while foraging and basking on elevated perches (e.g., fence posts, rocks, and shrubs). However, this species is shy, difficult to approach, and routinely bolts for safety under extremely dense thornscrub and *Opuntia* thickets (Montanucci, 1971); therefore, many individuals go totally unnoticed or are only discovered when disturbed. For these reasons, formal studies of habitat use in this species have been challenging.

Crotaphytus reticulatus was recently petitioned and precluded from federal listing under the Endangered Species Act (United States Fish and Wildlife Service, 2016), but it is listed as a state-threatened species in Texas (Hibbitts and Hibbitts, 2015). Most of the species' geographic distribution is limited to private lands in the Tamaulipan biotic province of southern Texas and adjacent Mexico (Fig. 1). The proliferation of exotic grasses, such as buffelgrass (*Cenchrus ciliaris*; Scott, 1996; Germano et al., 2001), and expanded gas and oil

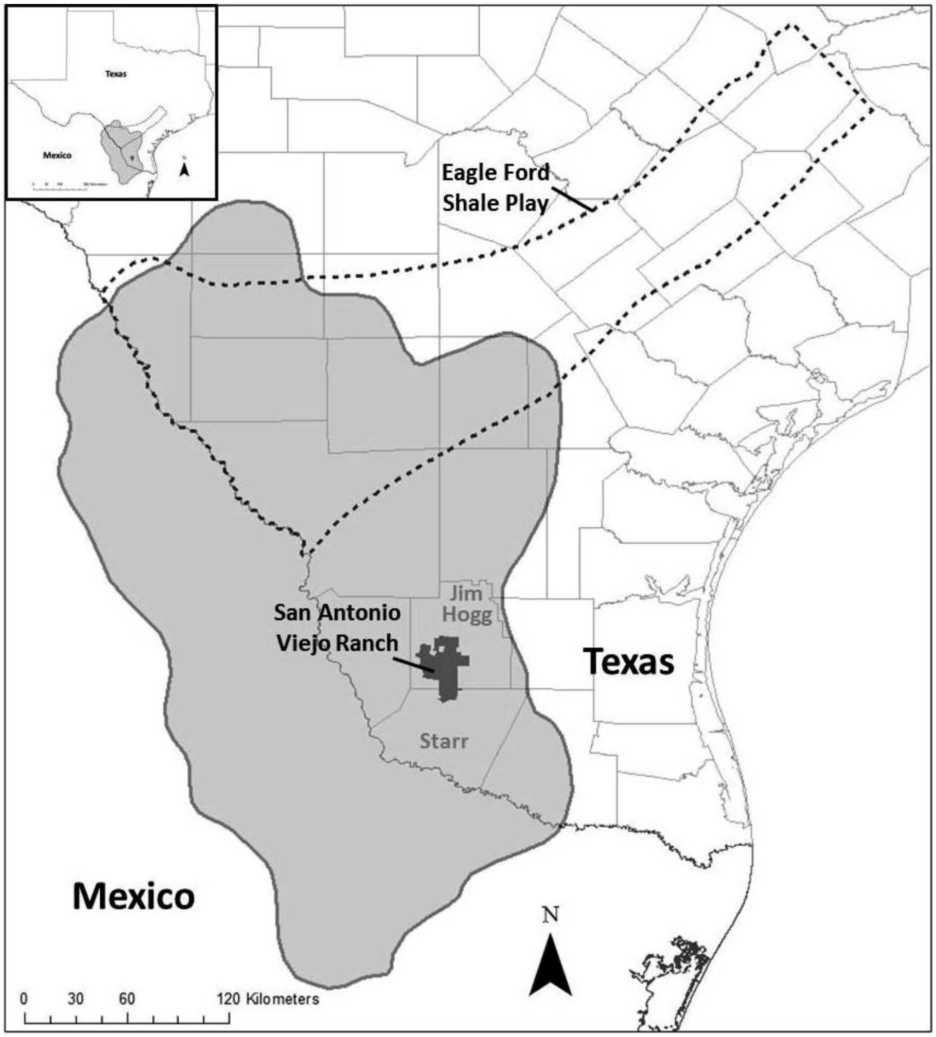

Fig. 1—Map of current reticulate collared lizard (*Crotaphytus reticulatus*) distribution (light gray) in Texas and Mexico. The study site (dark gray) was located on the East Foundation's San Antonio Viejo Ranch in Jim Hogg and northern Starr counties, Texas. Dashed line depicts the Eagle Ford Shale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

extraction (e.g., Eagle Ford Shale play; Wolaver et al., 2018) represent key conservation concerns for the species. We present the first study of diurnal and nocturnal microhabitat use in *C. reticulatus*. Results of this research provide a greater understanding of broad and fine-scale habitat relationships for this species that allow quantitative estimates of current habitat loss and degradation. These estimates can be used to identify regional conservation priorities for this species and enhance engagement with private landowners, who are the primary stewards for the species.

Materials and Methods—*Study Site*—We selected a site located on the East Foundation's San Antonio Viejo Ranch (SAVR) in Jim Hogg and northern Starr counties, Texas, USA (Fig. 1), which was known to contain a large population of *C. reticulatus*. This 61,000-ha cattle ranch represents a living laboratory dedicated to supporting wildlife conservation and other public benefits of ranching and private land stewardship. Within the study site, the *C. reticulatus* population occupies areas with typical Tamaulipan thornscrub habitat scattered across gravelly hills and loamy flats with characteristic plants that include mesquite (*Prosopis glandulosa*), several species of acacia (*Senegalia berlandieri, Vachellia rigidula, Vachellia tortuosa*), mimosa (*Albizia julibrissin*), paloverde (*Parkinsonia texana*), white brush (*Aloysia gratissima*), cenizo (*Leucophyllum frutescens*), and prickly pear (*Opuntia engelmannii lindheimeri*). Grasses such as *Bouteloua hirsuta* and hilaria (*Hilaria* spp.) are interspersed within the shrubs and small trees.

Telemetry—We conducted driving and walking surveys through the habitat described above 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 measured and recorded snout-to-vent length (SVL; millimeters) using a ruler, head width and length using calipers (millimeters), mass using Pesola® scales (grams), 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

TABLE 1—Telemetry summary for reticulate collared lizards equipped with Global Positioning System receivers and Very High Frequency telemetry radios on the East Foundation's San Antonio Viejo Ranch in Jim Hogg and Starr counties, Texas (2015–2016). SVL = snout-to-vent length.

Lizard	Sex	SVL (mm)	Mass (g)	Dates	Number of fixes
26	Male	99	47.0	30 June–10 July 2015	25
28	Female	116	51.5	16 March–18 April 2016	69
29	Male	112	51.0	17 March–24 March 2016	7
30	Male	105	50.5	17 March–16 April 2016	34
34	Male	115	61.0	27 April–11 May 2016	40
36	Male	113	61.0	19 May–3 June 2016	48
37	Male	116	71.0	19 May–2 June 2016	46
38	Female	105	54.0	19 May–26 May 2016	24
40	Female	107	47.0	18 May–29 May 2016	36
41	Male	121	69.5	3 June–27 June 2016	65

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 used braided fishing line 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. 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. We tracked 10 adult individuals (female:male ratio = 3:7) from 30 June to 10 July 2015 and from 16 March to 27 June 2016 (Table 1). The GPS transmitters were used for home range and movement analysis, which was not part of this study.

Microhabitat Site Selection—We used the VHF transmitters to home and visually observe lizards after dark with the purpose of identifying nocturnal microhabitat use sites. We located diurnal microhabitat use sites by driving slowly (~15 km/h) along ranch roads in the southwestern portion of SAVR. When a *C. reticulatus* was sighted, we marked the location with a pin flag and later returned to collect additional data detailed below. To characterize available microhabitats, at every 100 m along the survey route we walked 10 m into habitat on each side of the road whenever possible and selected an available microhabitat site.

Data Collection and Analysis—We characterized microhabitat available to each lizard using a meter-square frame centered over each lizard's positional data point (diurnal: $n = 73$; nocturnal: $n = 78$) and each systematically selected available microhabitat point ($n = 225$). At each of these points, we took a photo of the meter-square frame and later scored images for percent composition of the following categories: bare ground (e.g., dirt), woody plants, grass, forbs, debris (e.g., detritus), succulents, rocks (e.g., pebbles and gravel), and boulders (>200 mm).

We assessed microhabitat variables for multicollinearity. We found a significant pairwise Pearson correlation between pebbles and gravel ($R^2 = 0.45$, $P < 0.001$), so we combined those estimates of percent composition into a rock category. We tested for differences between diurnal, nocturnal, and random sites available to the lizard using multivariate analysis of variance (MANOVA) followed by pairwise comparisons among groups using Hotelling's post hoc tests of significance. We also used principal components analysis (PCA) to visualize the microhabitat characters that best distinguished between groups of sites. We conducted statistical analyses in PAST 3.07 (Hammer and Harper, 2006).

RESULTS—We found significant differences between all microhabitat site groupings in the MANOVA (Wilks' lambda = 0.416, $df_1 = 16$, $df_2 = 732$, F stat = 25.19, $P < 0.0001$). Using Hotelling's post hoc tests, we observed significant differences between all pairwise comparisons among groups of microhabitat sites ($P < 0.0001$ for random vs. diurnal, random vs. nocturnal, and diurnal vs. nocturnal). This pattern of statistical significance between microhabitat sites was apparent in the PCA (Fig. 2; Table 2). The first principal component axis explained 80.7% of the variation between microhabitat sites. Along this component, random microhabitat sites were composed of bare ground, grass, and forbs, and both diurnal and nocturnal microhabitat sites contained more woody plants, debris, succulents, rocks, and boulders (Fig. 2). Principal component two explained the remaining 19.3% of the variation between microhabitat sites (Table 2). Diurnal and nocturnal microhabitat sites separated along this component with diurnal sites containing more rocks and nocturnal sites containing more woody and succulent plants (Fig. 2).

DISCUSSION—We found that *C. reticulatus* used microhabitats with a gravel substrate and scattered boulders that were covered by a short overstory of woody and succulent plants rather than more heavily vegetated sites with dense grasses and forbs. This pattern of microhabitat use is consistent with previous habitat descriptions for the species that state that *C. reticulatus* occupies rolling terrain containing shallow, gravelly soils with moderately open to dense shrub cover and *Opuntia* thickets (Montanucci, 1971, 1976; Husak and Ackland, 2003). Unlike other Crotaphytids, *C. reticulatus* has been described as not inhabiting rock outcroppings in the region, which are instead occupied by the blue spiny lizard (*Sceloporus cyanogenys*; Montanucci, 1971). However, this study

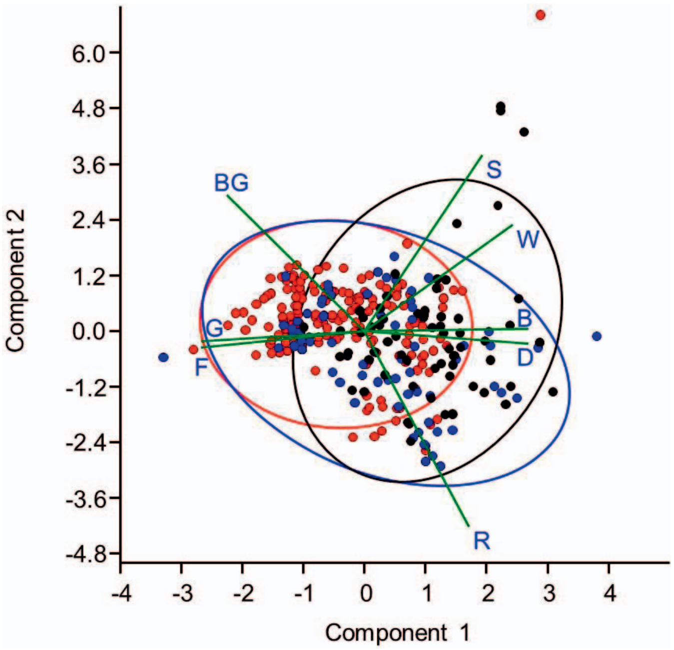

Fig. 2—Principal component analysis scatterplot of random microhabitat sites (red), diurnal sites (blue), and nocturnal sites (black) for reticulate collared lizards on the East Foundation's San Antonio Viejo Ranch in Jim Hogg and Starr counties, Texas (2015–2016). The vectors indicate the variable loadings for each microhabitat category on axis 1 and axis 2, and the ellipses represent 95% confidence intervals for each microhabitat site group. Microhabitat category abbreviations are as follows: bare ground (BG), woody plants (W), grass (G), forbs (F), debris (D), succulent (S), rocks (R), and boulders (B).

confirmed that *C. reticulatus* does use microhabitats with rocky outcrops and aggregations of boulders when they are present, even in sympatry with *S. cyanogenys*. This suggests that *C. reticulatus* is most likely perceived as being less saxicolous than other Crotaphytids because of the general lack of rocky outcrops available to *C. reticulatus* within the Tamaulipan thornscrub habitat.

We also found that *C. reticulatus* diurnal microhabitats were moderately open, shallow gravel slopes compared with nocturnal microhabitats, which contained dense thickets of woody and succulent plants. This daily shift in microhabitat use to dense, thorny plant cover at night was most likely a result of antipredator behaviors in *C. reticulatus* individuals that frequently lack the protective rock refuges that are an especially important habitat feature for Crotaphytids in general (Fitch, 1956). In fact, on many occasions *C. reticulatus* individuals were found sleeping on the surface within the cover of the dense vegetation as protection from potential predators (T.B.G. and C.S.A., pers. observ.). The degree to which the structure and dynamics of *C. reticulatus* populations are governed and limited by availability and characteristics of local rock habitats, as they are in other Crotaphytids (McGuire, 1996), is a worthy topic for future research. The open, gravelly characteristics of diurnal microhabitats with occasional vegetative structure were more consistent with microhabitat descriptions of other Crotaphytids, which as a group are visual predators that exhibit an ambush or sit-and-wait foraging style that requires some open spaces (Husak and Ackland, 2003).

Table 2—Loadings for each reticulate collared lizard microhabitat category in the principal components analysis illustrating multivariate differences between diurnal, nocturnal, and random sites on the East Foundation's San Antonio Viejo Ranch in Jim Hogg and Starr counties, Texas (2015–2016).

Category	Axis 1	Axis 2
Bare ground (dirt)	0.0355	−0.0002
Woody plants	0.0133	0.0026
Grass	0.0318	0.0180
Forbs	0.0452	0.0169
Debris (detritus)	−0.0560	0.0187
Succulent	−0.0319	−0.0955
Rocks (pebbles, gravel)	0.0164	0.0446
Boulders	−0.0543	−0.0052
Variance explained	80.7%	19.3%

Research concerning threats to *C. reticulatus* populations and habitat is lacking. However, given the strong convergence in life history between *C. reticulatus* and *Gambelia wislizenii* (Montanucci, 1971, 1978), inferences can be made from known threats to *G. wislizenii*. Both species have a preference for open foraging areas and an affinity for moderate shrub and forb cover with sparse grass cover (Steffen and Anderson, 2006). Invasion of exotic grasses is considered a major threat to *G. wislizenii* populations (Scott, 1996; Germano et al., 2001) and likely threatens *C. reticulatus* populations as well. Buffelgrass, for example, is planted as cattle forage in the lower Rio Grande Valley of southern Texas and northeastern Mexico (Franklin and Molina-Freaner, 2010; Tinoco-Ojanguren et al., 2016), and it is very successful at colonizing the open ground between shrubs and trees. Both *G. wislizenii* and *C. reticulatus* require these open areas for running during foraging and escape, so controlling the spread of invasive grasses is thought to be a conservation priority for each species. Buffelgrass was detected at our SAVR study site, which suggests that East Foundation's ranching practices and cattle grazing intensity may support *C. reticulatus* populations by alleviating potential negative effects of buffelgrass. Though anecdotal, this observation warrants additional research on the role of ranching practices in controlling the spread of invasive grasses and thus contributing to wildlife conservation.

Although historically considered uncommon within their Texas distribution, currently *C. reticulatus* populations are believed to be stable (United States Fish and Wildlife Service, 2016). This stability was most likely driven by two factors. First, nearly all *C. reticulatus* habitat was contained within large ranches in South Texas that restricted development. Second, ranching practices in the region have remained unchanged for decades where *C. reticulatus* populations are known to occur. This study confirms both of these notions because populations of *C. reticulatus* on East Foundation's SAVR showed all the signs of annual recruitment (i.e., gravid females and juveniles) and appeared robust over the 3-year study. Elsewhere in southern Texas, approximately 25% of the species' range occurs within the Eagle Ford Shale Play (Fig. 1). In this area, expanded gas and oil extraction has the potential to threaten *C. reticulatus* habitat and populations (Wolaver et al., 2018) through direct habitat loss from energy infrastructure (Hibbitts et al., 2013) or indirect effects of roads, traffic, and infrastructure on lizard behavior and mortality (Fahrig and Rytwinski, 2009; Hibbitts et al., 2017).

Herein, we characterize habitat relationships for *C. reticulatus* that will allow quantitative estimates of future habitat loss and degradation. Perhaps more importantly, this study recognizes that private land stewardship across the *C. reticulatus* distribution in Texas has benefitted the species by maintaining habitat used by the lizard. As such, future conservation actions for the species will be most successful with continued engagement with private landowners, who are the primary stewards for the species.

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