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Spatiotemporal Patterns of Snake Captures and Activity in Upland Pine Forests

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ABSTRACT.—Patterns of species' occurrences across space and time are fundamental components to understanding their ecology, as this variation often reflects responses to local environmental gradients. We built species-specific models to understand the spatial and temporal factors predicting captures and activity of five snake species in upland pine forests: copperhead (*Agkistrodon contortrix*), racer (*Coluber constrictor*), coachwhip (*Masticophis flagellum*), western ratsnake (*Pantherophis obsoletus*), and western ribbonsnake (*Thamnophis proximus*). From mid-May to mid-July across 3 y (2018, 2019, 2020), we monitored boxtraps in two upland pine forests experiencing different management regimes: (1) subjected to frequent thinning and prescribed burning, and (2) subjected to infrequent thinning and prescribed burning. Significantly more copperheads and western ribbonsnakes were captured at the infrequently thinned and burned forest, whereas significantly more racers were captured at forest subjected to frequent thinning and burning. As the summer progressed, captures decreased each subsequent month for both racers and western ratsnakes, with the fewest captures in July. Western ratsnakes were the only species to exhibit a response to the weather in that activity decreased with increasing rainfall. No variables were significant predictors of coachwhip captures. The variation in captures across space may be attributed to the physiological tolerances of each species based on their habitat preferences or differences in prey availability at each forest. Interactions between the physiological tolerances, foraging behaviors, or their reproductive phenology may be underlying the temporal variation in activity patterns.

INTRODUCTION

Central components to understanding an animal's ecology are its habitat associations and activity patterns (Pianka, 1994). Anthropogenic activities that alter the structural components of habitats can have cascading effects on resources, such as food and habitat availability, which in turn, can alter behaviors, populations, or communities (Kilpatrick *et al.*, 2010; Earl *et al.*, 2017; Matich and Schalk, 2019; Cordier *et al.*, 2021). Activity patterns are the result of the interplay between both intrinsic and extrinsic factors. Extrinsic factors underlying activity patterns can be attributed to variation in abiotic factors (*e.g.*, rainfall, temperature) or abundance of resources (*e.g.*, prey availability; Tinkle, 1957; Brown and Shine, 2002; Schalk and Saenz, 2016). Intrinsic factors that underlie the activity patterns of a species are associated with their physiological tolerances or reproductive biology (*e.g.*, mate searching behaviors, migration to or dispersal from breeding ponds; Timm *et al.*, 2007; Sosa and Schalk, 2016; Lutterschmidt *et al.*, 2019).

In North America many snakes have extensive geographic ranges, spanning multiple ecosystems arrayed across a diversity of environmental and anthropogenic gradients (Powell

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et al., 2016). These widespread species can exhibit adaptive responses across these landscapes resulting in intraspecific variation in their ecology and physiology (Dix, 1968; Smith *et al.*, 2009; Weatherhead *et al.*, 2012). Variation in occurrence of these wide-ranging species across space is strongly correlated to the landscape cover or the land-use practices that alter the resource abundance used by these species as well as affect the strength of interspecific interactions between co-occurring species (Steen *et al.,* 2012; Steen *et al.,* 2014; Doherty *et al.*, 2020; Cordier *et al.*, 2021). The seasonal patterns of snake activity in temperate zones are well documented (Gibbons and Semlitsch, 1987). Short-term activity patterns of snakes are more variable due to interspecific variation in the natural histories, but are often correlated with abiotic factors (Eskew and Todd, 2017). However, snakes possess several attributes, including extended periods of inactivity and their inconspicuous nature, that make assessments of their ecology particularly challenging (Parker and Plummer, 1987; Steen, 2010; Durso *et al.*, 2011).

In the southern United States, pine forests are managed for a variety of ecosystem services (*e.g.*, carbon sequestration, timber production, support of biodiversity; Fox *et al.*, 2007; Mori *et al.*, 2017). Management practices (*e.g.*, prescribed fire, mechanical operations) can alter structure and successional trajectories of forests, which can have cascading effects on resource availability. For example, reintroduction of fire to disturbance dependent ecosystems can alter the diversity and biomass of vegetative communities, subsequently habitat availability as well as prey assemblages (Bowman and Legge, 2016; Adams, 2021). Frequent fires also help maintain open canopies providing thermoregulatory opportunities for ectotherms, such as snakes (Howze and Smith, 2021). Given the sensitivity of reptiles to changes in land-use and the geographic variation in their life histories (Smith *et al.,* 2009, Cordier *et al.,* 2021), efforts that utilize a comparative approach to analyze spatiotemporal patterns of captures and activity can help develop current population estimates while also helping predict future population trends.

We quantified the spatial and temporal factors correlated with activity and captures of snakes in two upland pine forests subjected to different forest management regimes across three summers (May–June/July; corresponding to the season of peak snake annual activity). We focused on five species that were commonly encountered in our trapping efforts (copperhead [*Agkistrodon contortrix*], racer [*Coluber constrictor*], coachwhip [*Masticophis flagellum*], western ratsnake [*Pantherophis obsoletus*], and western ribbonsnake [*Thamnophis proximus*]). We explored species-specific models to determine if interspecific patterns in captures (our measure of snake activity) could be explained by spatiotemporal predictors. Given their secretive nature, emerging threats, and their global risk of decline (Reading *et al.*, 2010; Lorch *et al.*, 2016), it is critical to determine the similarities and differences between these species to not only further refine our understanding on their ecologies, but also to inform and develop predictions as to how these species may respond to environmental changes.

METHODS

STUDY AREA

Snakes were trapped as part of a larger effort exploring the structure and function of snake assemblages at two forests under different forest management regimes in the West Gulf Coastal Plain of east Texas (*see* Adams, 2021 for more details). South Boggy Slough Conservation Area (SBSCA; 31°17′45″N, 94°55′37″W) is owned and operated by the T.L.L. Temple Foundation and is subjected to frequent prescribed burns (1–3 y fire intervals) as

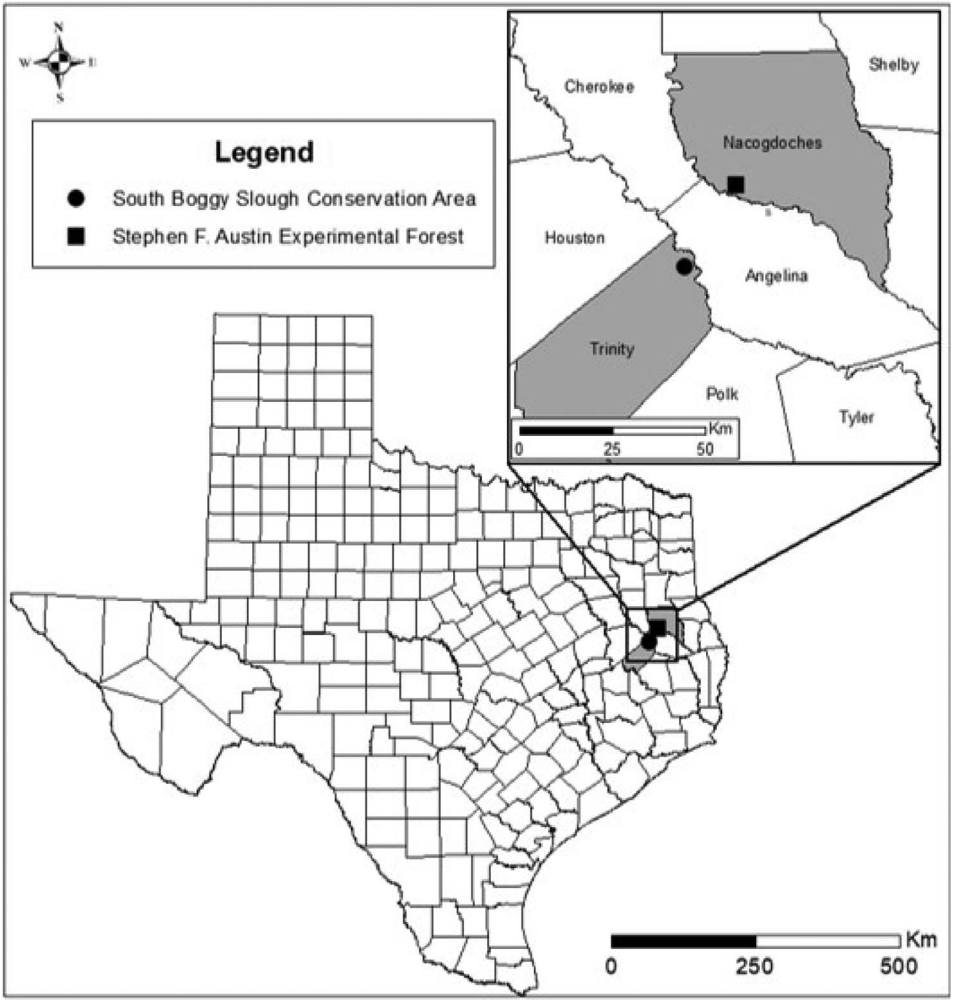

FIG. 1.—Location of the study sites in east Texas, U.S.A. Each site is subjected to different forest management regimes where South Boggy Slough Conservation Area has shorter burn return fire intervals and thinning operations while the Stephen F. Austin Experimental Forest has longer intervals between prescribed fires and thinning operations

well as thinning and regeneration harvest (R. Sanders, pers. comm.; Fig. 1). The resulting habitat has an understory with high herbaceous cover, primarily grasses, sedges, and forbs, and a low basal area, predominately comprised of shortleaf pine (*Pinus echinata*) with southern red oak (*Quercus falcata*) interspersed infrequently throughout the area (Adams, 2021). The Stephen F. Austin Experimental Forest (SFAEF; 31°30′11″N, 94°46′16″W) is owned and operated by the U.S. Forest Service and is subjected to burn intervals every 5–8 y and very few harvesting operations within the last 50 y (D. Saenz, unpubl. data). The resulting habitat has a high basal area with a closed canopy comprised of a mix of *P. echinata*

TABLE 1.—Trapping period and effort for boxtraps deployed at South Boggy Slough Conservation Area (SBSCA) and the Stephen F. Austin Experimental Forest (SFAEF)

Site	Year	Site	Traps opened	Traps closed	# Trap days
SBSCA	2018	SBSCA	28 May 2018	20 July 2018	370
	2019	SBSCA	27 May 2019	17 July 2019	380
	2020	SBSCA	11 May 2020	26 June 2020	380
SFAEF	2019	SFAEF	19 May 2019	17 July 2019	350
	2020	SFAEF	11 May 2020	26 June 2020	350

and loblolly pine (*Pinus taeda*) with a higher abundance of red oak species (*Quercus* sect. *lobatae*). Compared to SBSCA, the midstory and understory at SFAEF are much denser and predominately comprised of American sweetgum (*Liquidamber styraciflua*) and American beautyberry (*Callicarpa americana*; Adams, 2021).

SNAKE TRAPPING

Boxtraps (n = 10 per forest management type; 20 box traps total; Burgdorf *et al.*, 2005) were installed at least 450 m apart from one another in each forest type (*i.e.*, site). Each boxtrap array consisted of four hardware cloth drift fences (length = 15 m; mesh size = 6.4 mm) and four pitfall traps (18.9 L) at the end of each drift fence. We opened traps in summer months (May, June, July) that coincide with peak activity of terrestrial snake species in this region (J. Pierce, unpubl.; Table 1). At SBSCA traps were monitored across 2018, 2019, and 2020 snake activity seasons (Table 1). At the SFAEF traps were monitored across 2019 and 2020 (Table 1). Traps were checked daily between the hours of 0730h and 1130h and closed when daily checks were not feasible. Prior survey efforts in this region suggest that snakes may exhibit trap avoidance over time (J. Pierce, unpubl. data), therefore to minimize trap avoidance and maximize capture success, we moved each box trap at least 100 m from its location in the previous summer. Snakes were processed in the lab where they were marked using medical cautery units (Winne *et al.* 2006) and released the following day.

WEATHER DATA

To explore the relationships between weather patterns and snake activity, we collected abiotic variables from local weather stations to include in our models. Three abiotic variables were included: (1) maximum daily temperature (C), (2) minimum daily temperature (C), and (3) daily rainfall (mm). The SBSCA site was midway between two weather stations located at the Angelina County airport (31°14′9″N, –94°45′15″W; approximately 18 km away) and the U.S. Forest Service RAWS weather station in Ratcliff, TX (31°23′42″N, 95°8′9″W; approximately 22 km away). Average minimum and maximum temperatures within the study periods were similar between these two weather stations used for the SBSCA weather data. However, the Ratcliff, TX site was wetter during the trapping period across all 3 y (both in terms of average daily precipitation and total precipitation); therefore, we averaged the weather data between these two weather stations to use in our analyses of snake activity at SBSCA. Weather data for the SFAEF was obtained from a single weather station in Nacogdoches, TX (31°36′58″N, 94°38′34″W; approximately 17 km away).

TABLE 2.—Captures of five snake species (copperhead [*A. contortrix*], racer [*C. constrictor*], coachwhip [*M. flagellum*], western ratsnake [*P. obsoletus*], and western ribbonsnake [*T. proximus*]) in boxtraps at South Boggy Slough Conservation Area (SBSCA) and the Stephen F. Austin Experimental Forest (SFAEF) across three summer seasons. No boxtraps were deployed in 2018 at the SFAEF. Recaptured individuals are pooled within these values (see methods for details)

Site	Year	Copperhead	Racer	Coachwhip	Western ratsnake	Western ribbonsnake	Total
SBSCA	2018	20	12	7	10	12	61
	2019	13	19	5	12	8	57
	2020	10	23	4	12	13	62
SFAEF	2019	45	5	2	13	21	86
	2020	39	7	2	8	26	82
Total		127	66	20	55	80	

DATA ANALYSIS

Data were first analyzed by daily captures, but failed due to too many zeros. Data were then organized by total weekly (within month and year) captures of each snake species. The response variable, y, is total weekly captures of each snake species, and, therefore, is assumed to follow a Poisson distribution. Thus, data were analyzed using the following log-linear model:

$$y_{ijkl} = \mu + SITE_i + YEAR_j + MONTH_k + MAXTEMP_{ijk} + MINTEMP_{ijk} + PRECIP_{ijk} + \varepsilon_{ijkl},$$

where y_{ijkl} is the log scale of the count of copperheads, racers, coachwhips, western ratsnakes, or western ribbonsnakes, respectively, of the ith site, jth year, kth month and lth replicate (week). $SITE_i$, $YEAR_j$, and $MONTH_k$ were the effects of the ith site, jth year, and the kth month, respectively. MAXTEMP, MINTEMP, and PRECIP were the weekly averages of the maximum daily temperature, minimum daily temperature and daily precipitation, respectively. We did not include all interactions in the model, given our preliminary analyses suggested that they were not significant. Data were analyzed using SAS Proc Genmod procedure (Stokes *et al.*, 2000). Preliminary analyses found that there is enough data to justify the number of parameters in each model, but over-dispersion was an issue for all response variables; therefore, we used a negative binomial distribution, which has the same mean structure as Poisson regression, but paired with an extra parameter to model over-dispersion. We used the "ilink" option (for inverse link) to obtain the predicted count in addition to the linear predictions. Across all years and trapping periods, three individuals of the focal species were recaptured at SBSCA (one copperhead, one racer, and one coachwhip) and two individuals of the focal species were recaptured at SFAEF (one western ratsnake and one western ribbonsnake). These recaptures were included in our analyses. Finally, to visualize snake activity patterns across each forest and year, we created presence/absence plots of daily captures during each trapping period.

RESULTS

We captured a total of 343 unique individuals (plus five recaptures) of the five focal snake species across 1830 trap days (Table 2). Copperheads had the broadest activity window with at least one capture on 77 d across all sites and years, whereas coachwhips had the narrowest window and were only captured on 16 d across all sites and years (Fig. 2). We observed no inter-annual variation in captures or activity among species (Tables 2, 3). We captured

TABLE 3.—Parameter estimates of weekly captures of five snake species from upland pine forests at South Boggy Slough Conservation Area (SBSCA) and the Stephen F. Austin Experimental Forest (SFAEF). Significant relationships are depicted in bold

	Parameter estimates					
Species and effect	Variable	Estimate	SE	df	t value	Pr > $\lvert t \rvert$
Copperhead (*A. contortrix*)	Intercept	−0.49	2.05	29	−0.24	0.81
Site	SBSCA	−1.45	0.26	29	−5.5	<**0.01**
	SFAEF	0.00				
Year	2018	0.24	0.43	29	0.56	0.58
	2019	0.03	0.29	29	0.11	0.91
	2020	0.00				
Month	May	0.00				
	June	0.05	0.27	29	0.18	0.86
	July	0.18	0.37	29	0.48	0.64
	Max. temp.	0.08	0.08	29	1.05	0.30
	Min. temp.	−0.02	0.08	29	−0.19	0.85
	Precipitation	−0.04	0.03	29	−1.12	0.27
Racer (*C. constrictor*)	Intercept	−3.21	2.71	29	−1.18	0.25
Site	SBSCA	1.12	0.33	29	3.4	<**0.01**
	SFAEF	0.00				
Year	2018	−0.80	0.46	29	−1.75	0.09
	2019	0.17	0.33	29	0.52	0.6
	2020	0.00				
Month	May	0.00				
	June	−0.24	0.30	29	−0.8	0.43
	July	−2.28	0.68	29	−3.37	<**0.01**
	Max. temp.	0.11	0.11	29	1.01	0.32
	Min. temp.	0.01	0.11	29	0.07	0.94
	Precipitation	−0.07	0.05	29	−1.38	0.18
Coachwhip (*M. flagellum*)	Intercept	−0.23	4.86	29	−0.05	0.96
Site	SBSCA	0.58	0.61	29	0.95	0.35
	SFAEF	0.00				
Year	2018	0.92	0.87	29	1.06	0.30
	2019	0.55	0.67	29	0.82	0.42
	2020	0.00				
Month	May	0.00				
	June	0.22	0.60	29	0.37	0.71
	July	−1.12	1.03	29	−1.1	0.28
	Max. temp.	0.03	0.18	29	0.18	0.86
	Min. temp.	−0.11	0.20	29	−0.53	0.60
	Precipitation	−0.07	0.09	29	−0.74	0.47
Western ratsnake (*P. obsoletus*)	Intercept	1.97	2.85	29	0.69	0.50
Site	SBSCA	0.11	0.30	29	0.38	0.71
	SFAEF	0.00				
Year	2018	−0.05	0.54	29	−0.09	0.93
	2019	0.52	0.37	29	1.39	0.18
	2020	0.00				
Month	May	0.00				
	June	−0.42	0.29	29	−1.44	0.16
	July	−2.19	0.59	29	−3.74	<**0.01**
	Max. temp.	−0.17	0.12	29	−1.41	0.17
	Min. temp.	0.22	0.12	29	1.86	0.07
	Precipitation	−0.15	0.06	29	−2.65	**0.01**

TABLE 3.—Continued

Species and effect	Variable	Estimate	SE	df	*t* value	Pr > |*t*|
	Parameter estimates					
Western ribbonsnake (*T. proximus*)	Intercept	3.30	2.12	29	1.56	0.13
Site	SBSCA	−0.97	0.27	29	−3.55	**<0.01**
	SFAEF	0.00				
Year	2018	0.24	0.47	29	0.51	0.61
	2019	−0.20	0.32	29	−0.64	0.52
	2020	0.00				
Month	May	0.00				
	June	−0.32	0.28	29	−1.16	0.26
	July	−0.45	0.40	29	−1.13	0.27
	Max. temp.	−0.11	0.09	29	−1.18	0.25
	Min. temp.	0.08	0.09	29	0.95	0.35
	Precipitation	−0.04	0.04	29	−0.93	0.36

significantly more copperheads and ribbonsnakes at the SFAEF compared to SBSCA, and observed the opposite pattern for racers (Tables 2, 3). No site differences were observed for the other species (Table 3). Racers and western ratsnakes exhibited a significant difference in monthly activity patterns (Table 3). We captured significantly fewer racers and western ratsnakes in July, whereas coachwhips and ribbonsnakes exhibited a similar, but nonsignificant, trend (Table 3). Copperhead activity did not decline intra-annually (Table 3). Western ratsnake activity decreased with increasing rainfall and was the only species to exhibit a significant response to the weather (Table 3). None of the spatial, temporal, or abiotic factors was a significant predictor of coachwhip activity (Table 3).

DISCUSSION

Forest type was a strong predictor of snake captures in four of the five species in our study, possibly due to differences in vegetation structure, which could have had cascading effects on resource availability. Although trap properties can affect capture and retention of target taxa (Willson *et al.*, 2008; Luhring *et al.*, 2016), we used the same sampling technique and effort, making our sampling feasible to compare sites and years. Therefore, the observed patterns within our sampling period are likely due to their differences in their capture rate and activity across space and time. The high captures of four of the five target species (coachwhips being the exception) enabled us to develop models assessing the potential causes underlying their variation across space and time.

SPATIAL VARIATION IN CAPTURES

Copperheads are geographically widespread generalists that utilize a variety of resources along both their dietary and habitat niche axes (Fitch, 1960; Gloyd and Conant, 1990; Ford *et al.*, 1991; Lagesse and Ford, 1996; Schalk *et al.*, 2018). At our study sites, forest management practices shifted the prey base as crickets, anurans, lizards, and spiders were more abundant at the SFAEF, whereas grasshoppers and small rodents were more abundant at SBSCA (Adams *et al.*, 2022). Although the differences in prey quality (Weidler and Lutterschmidt, 2021; Willson and Hopkins, 2011) from these sites are unknown, all of the

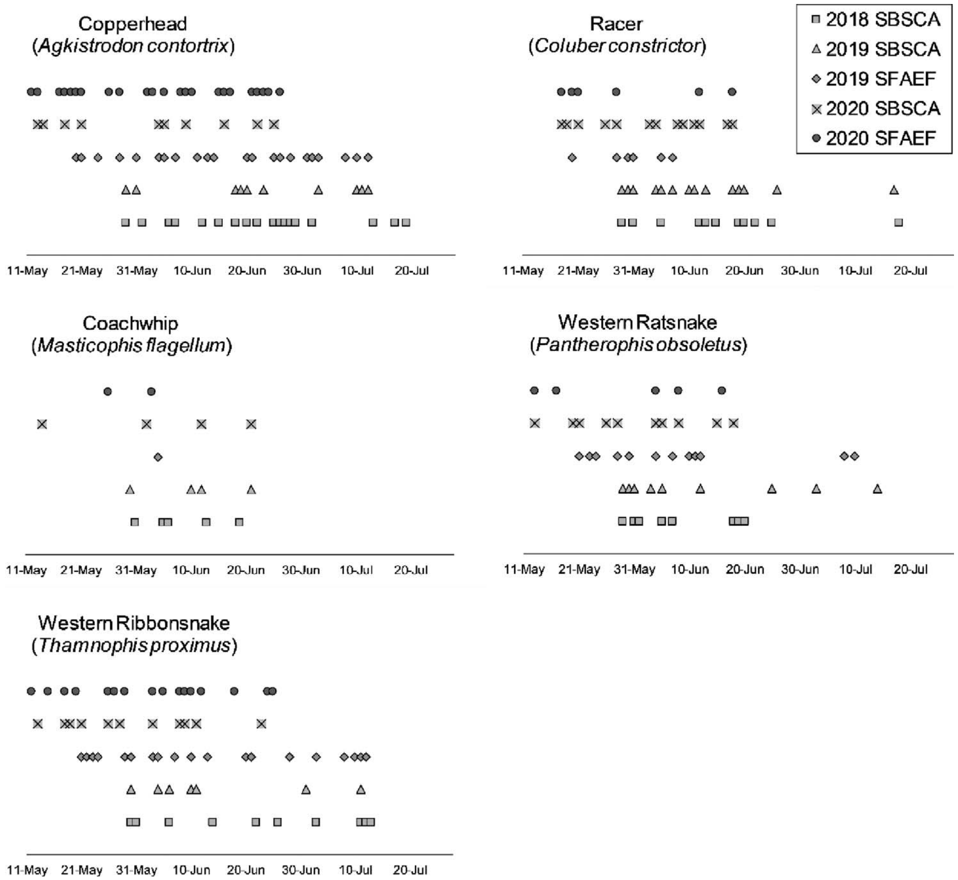

FIG. 2.—Daily snake captures for the five focal species vs. date at South Boggy Slough Conservation Area (SBSCA) and the Stephen F. Austin Experimental Forest (SFAEF) across three summer seasons. See Table 1 for details on trapping periods and effort

aforementioned taxa are preyed upon by copperheads (Fitch, 1960; Gloyd and Conant, 1990; Lagesse and Ford, 1996; Schalk *et al.*, 2018). As a result, shifts in the prey base seem an unlikely mechanism driving the shifts in captures across these two sites. However, copperheads in the southern United States do exhibit a preference for habitats with greater canopy cover and leaf litter that create moister microhabitats (Fitch, 1960; Steen *et al.*, 2012; Novak *et al.*, 2020). SFAEF has greater leaf litter depth and canopy cover that is more homogenously distributed across the landscape, resulting in greater availability of preferred copperhead microhabitats (Adams, 2021). In managed forests, copperheads tend to prefer habitats with greater leaf litter depth and coarse woody debris (Sutton *et al.*, 2017). If those microhabitats are unavailable due to prescribed burning, copperheads will use shrub thickets (Flaherty and Gienger, 2020). The frequent thinning and prescribed burning at SBSCA reduced the amount of leaf litter available and created more coarse woody debris, resulting in patches of suitable microhabitats intermittently distributed across the landscape (Adams *et al.*, 2022); thus, allowing copperheads to persist, despite the absence of their most preferred microhabitats, albeit perhaps at lower population densities. Even though coarse woody debris are thermally-stable and moist refugia that support suitable prey that can be utilized by copperheads (Whiles and Grubaugh, 1996), there is a greater availability of suitable microhabitats at the SFAEF, likely underlying the higher captures of copperheads when compared to the SBSCA.

Similar to copperheads, racers utilize multiple habitat types across their range (Fitch 1963 and references therein), but unlike copperheads, racers tend to use open or forest edge habitats rather than forest interiors (Plummer and Congdon, 1994; Carfagno and Weatherhead, 2006; Howley *et al.*, 2016). Our results are consistent with these prior studies, as more racers were captured at SBSCA. In Kentucky, Howey *et al.* (2016) monitored racers in unburned and burned plots and captured nearly twice as many individuals in burned plots and found that radio tagged racers preferred more open habitats. The exclusion of fire resulted in higher canopy cover and leaf litter depth in the unburned plots, whereas tree density was lower and grass and forb cover were higher in the burned plots, altering thermoregulatory opportunities for snakes in these areas (Howley *et al.*, 2016). These characteristics are also reflective of the habitat at SBSCA, which could result in a more optimal thermal landscape and increased thermoregulatory opportunities for racers at SBSCA compared to SFAEF. In addition to thermoregulatory opportunities, shifts in the prey base may be affecting racer capture rate across these two forests. The predominant prey species for racers are small vertebrates and larger insects (*e.g.*, grasshoppers; Fitch, 1963; Shewchuk and Austin, 2001; Halstead *et al.*, 2008), both of which were more abundant at SBSCA than the SFAEF (Adams *et al.*, 2022). The higher availability of their preferred prey at SBSCA may increase their foraging success, resulting in more captures at SBSCA.

Western ribbonsnakes exhibit a high affinity for mesic habitats (*e.g.*, small pools, ditches; Tinkle, 1957; Clark, 1974). Small pools that form on surface soils are important to ribbonsnakes as these pools serve as breeding habitats for their amphibian prey as well as provide a physiological refuge from desiccation (Fitch, 1949; Clark, 1974; Hampton, 2008). The higher canopy cover and increased leaf litter and duff layers at the SFAEF (Adams, 2021) created wetter microhabitats that are more suitable to ribbonsnakes, likely driving their higher capture rate at this site. The thinning and burning practices at SBSCA reduced tree density and leaf litter on the landscapes, creating more xeric conditions that are less suitable for ribbonsnakes. In their comparison of snake diversity across three forest habitats in east Texas, Ford *et al.* (1991) captured no ribbonsnakes in the upland coniferous forest, whereas the majority of captured occurred in the lowland floodplain forest. Although we captured fewer ribbonsnakes at SBSCA compared to the SFAEF, they were still captured fairly frequently at SBSCA. Logging operations at SBSCA utilized skidders that form trails and compact soil, creating ephemeral pools utilized as breeding sites by amphibians (Cromer *et al.*, 2002; DiMauro and Hunter, 2002; pers. obs.). Ribbonsnakes likely exploit these temporary pools for food and refuge, which could explain their presence in these upland pine forests.

We did not observe any significant spatial variation in captures of coachwhips or western ratsnakes across the two study sites. We would expect to capture more coachwhips at SBSCA, as they prefer more open habitats in east Texas where they can thermoregulate and forage efficiently (Johnson *et al.*, 2007). However, the small sample sizes and the statistical challenges of studying snakes are well known (Steen, 2010), and the low number of coachwhip captures is likely underlying the lack of any discernable patterns in captures across these two sites. In eastern Texas, western ratsnakes can utilize a variety of habitats (Ford *et al.*, 1991), but are typically associated with more mesic habitats, such as bottomland hardwood forests (Pierce *et al.*, 2008; Steen *et al.*, 2012). Thus, the habitat conditions of these upland pine forests may not provide optimal habitat conditions preferred by this species. Both study sites have large tracts of bottomland hardwood forests, and expanded trapping efforts in this habitat may clarify our apparent lack of habitat effect observed in this study. Western ratsnakes do exhibit shifts in habitat use across time, which is primarily attributed to seasonal shifts in their thermoregulatory behavior, and prefer more open canopy sites in the early spring and summer, shifting to forest edges in later summer (George *et al.*, 2017). The temporal scale in which we conducted our surveys precludes us from capturing snakes potentially undertaking these seasonal movements.

TEMPORAL VARIATION IN CAPTURES AND ACTIVITY

As the summer progressed, snake activity declined and this pattern was significant for both racers and western ratsnakes. In this region of the United States (east Texas and western Louisiana), snake ecologists have long recognized the “snake season” as ranging from March through June (Fitch, 1949; J. Pierce, unpubl.). These higher activity levels coincide with emergence from hibernacula as well as mate searching behaviors, as males seek out females (Tinkle, 1957; Lutterschmidt *et al.*, 2019). July coincides with the end of the breeding season for many of these species (Seigel and Ford, 1987), and the reduced activity may be attributed to the cessation of these mate searching behaviors.

On an annual scale, snake activity increases with increasing temperatures (Eskew and Todd, 2017), but the high daytime temperatures during July may exceed the species’ thermal activity thresholds (Peterson *et al.*, 1993; Gunderson and Leal, 2015), resulting in the decreased activity observed in the later summer months. In their study of activity patterns of western ratsnakes, George *et al.* (2015) observed a similar pattern in which snake activity was lowest mid-summer and peaked at 30 C. The 30 C threshold has been determined to be the preferred body temperature of western ratsnakes from Texas (Weatherhead *et al.*, 2012). Ratsnakes are efficient thermoregulators (Weatherhead *et al.*, 2012) and exhibit behavioral plasticity, becoming increasingly nocturnal in their foraging, if it coincides with their optimal temperature (DeGregorio *et al.*, 2014). Our weekly average of temperatures may have been too coarse of a measure to detect any significant relationships, but maximum temperatures almost always exceeded 30 C during July, likely constraining western ratsnake activity at our study sites. Racers are much less plastic in their foraging behavior, and are obligate diurnal foragers (DeGregorio *et al.*, 2014). At these sites, the high daytime temperatures in July likely created smaller foraging windows in which racers could be active. Copperheads, the only species to not follow this trend, tend to not thermoregulate as efficiently as other snakes (Harvey and Weatherhead, 2011; Weatherhead *et al.*, 2012; Mueller and Gienger, 2019). Rather, copperheads undergo seasonal shifts in their thermal ecology and become increasingly nocturnal as the daytime temperature increases during summer (Sanders and Jacob, 1981). Although we only checked traps once per day, the continued captures late in the summer may be a result of copperheads seeking thermal refuge through their increasingly nocturnal behavior.

In the southeastern United States, increased precipitation can reduce activity for more terrestrial snakes as their prey do not increase in abundance or activity with increased rainfall (Eskew and Todd, 2017). During the period of our study, precipitation reduced the activity for western ratsnakes. Western ratsnakes have an increased propensity for climbing during summer months in this region (Pierce *et al.*, 2008), where they prey upon birds and mammals (Rudolph *et al.*, 2009). Increased rainfall may reduce prey activity and reduce foraging success by obscuring the visual and chemical cues ratsnakes use to locate prey (Mullin and Cooper, 1998; Mullin and Cooper, 2000).

CONCLUSIONS

Our results suggest that capture and activity patterns of snakes are influenced by local environmental gradients. Forest management practices are altering local resources that, in turn, are underlying the observed variation in captures of species across these two sites. Future efforts could focus on more expansive trapping across multiple sites with more varied forest management regimes to provide a more nuanced pattern on how these species are responding to the emergent habitat and resource gradients. Further, whereas our study was conducted during the period that coincides with peak snake activity in this region (Fitch, 1949), snakes are still active across much of the year (Ford *et al.*, 1991; Johnson *et al.*, 2007; Pierce *et al.*, 2008). Expanding the length of the survey period would provide insights as to how species' activity correlates with the resources, such as prey or thermal gradients, that exhibit strong variation in their availability at larger temporal scales.

Both spatial factors, such as forest type, and temporal factors, such as rainfall, can affect the captures and activity patterns of snakes, depending on the species. Specifically, we captured significantly more copperheads and ribbonsnakes in the forest subjected to infrequent thinning and burning, and significantly more racers at the forest subjected to frequent thinning and burning. We also observed intra-seasonal declines in activity for racers and western ratsnakes as summer progressed. At an even smaller temporal scale, western ratsnake activity was negatively correlated with rainfall. Although these species are widespread, the patterns observed in our study appear to reflect their preferred habitats and optimal resources in specific parts of their range. Future efforts that test the proposed causal mechanisms in the context of the physiological constraints and resource demands of these species (Sears *et al.*, 2011; Perkins *et al.*, 2020) would not only provide support for the mechanisms driving this variation, but can also be used to inform conservation efforts (Shoemaker *et al.,* 2009). Altogether, these results provide insights into how snake populations may shift in response to land-use practices and environmental factors and can be used to inform monitoring efforts of these elusive species.

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