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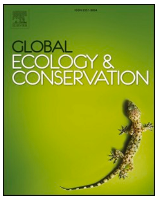

Small nature preserves do not adequately support large-ranging snakes: Movement ecology and site fidelity in a fragmented rural landscape

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ABSTRACT

Habitat fragmentation and loss are two of the leading causes of species declines world-wide. To mitigate these effects, land managers have engaged two major pathways to conserve biodiversity: land-sparing (set aside for wildlife and conservation) or land-sharing (land is managed to provide benefits for multiple land uses). We examined the movement ecology of a wide-ranging snake in a fragmented landscape as a case study to examine the efficacy of small nature preserves to protect threatened biodiversity. We monitored the movement patterns and habitat use of 25 timber rattlesnakes (*Crotalus horridus*) over the course of four years in a small nature preserve and fragmented agricultural landscape in central Tennessee, USA. Rattlesnakes showed a positive association with rocky cedar barrens and glades, habitat edges, and sites with dense ground cover and relatively open canopy cover. In addition, 49% of all rattlesnake locations fell outside the nature preserve boundary. Most rattlesnakes travelled through the nature preserve and into patchy agricultural areas and rural housing properties while foraging for food and searching for mates. The conservation of species, especially those that have large movement patterns or migratory behaviors, are difficult to protect in a land-sparing or protected area scenario. We highlight that while the nature preserve does not adequately contain timber rattlesnakes throughout the year, it does support the conservation of key habitat for overwintering, which is essential for the survival of this species. A combination of land-sparing and land-sharing are required for the protection and management of this and many other species.

1. Introduction

Habitat fragmentation is one of the leading threats to wildlife world-wide (Fahrig, 2003; Fischer and Lindenmayer, 2007). Human population growth and related land uses place ever-growing pressure on wildlife as suitable habitats become smaller and more disconnected. While many species have adapted to anthropogenic landscapes and survive in disturbed environments (Kark et al., 2007; Lowry et al., 2013; Nordberg and Schwarzkopf, 2019), other species are more sensitive to environmental change and suffer population

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declines (Blair, 1996; Neilly et al., 2018). Direct loss of habitat through land clearing for agriculture, human developments, or other industrial projects displace many species permanently; however, roads and other relatively small-scale land clearings can have large effects on populations as well (Andrews, 2007; DeGregorio et al., 2010). For example, roads can pose as physical and genetic barriers, limiting the dispersal and genetic flow among populations (Clark et al., 2010; Shepard et al., 2008).

In recent decades, many conservationists and land managers have engaged in a debate on how best to preserve species, predominantly through one of two pathways: land-sparing, or land-sharing (Kremen, 2015; Law and Wilson, 2015). The practice of land-sparing involves maintaining native undisturbed habitats specifically for nature conservation (Fischer et al., 2008; Phalan et al., 2011). These areas are often national parks, wildlife refuges, or nature conservation areas that are protected from development or disturbance to maintain native habitat for wildlife. Alternatively, the act of land-sharing maintains landscapes that can be suitable for multiple uses, including wildlife conservation (Fischer et al., 2008; Phalan et al., 2011). Supporters of land-sharing argue that few areas remain as protected areas (14.7% of global land area), compared to other landscapes, such as agricultural landscapes (e.g. 48.6 million km^2 [37.4% of global land area; World Bank Group, 2016]) that could be used to help promote conservation. If properly managed, some agricultural landscapes can support high biodiversity and accumulate benefits for industry and wildlife conservation simultaneously on the same land (Neilly et al., 2016).

Because of the finite amount of natural habitat remaining, it becomes increasingly difficult to protect mobile species. Regardless of how large a protected area is, there will always be species and individuals that, quite literally, live on the edge, making it difficult to provide adequate protection (Borowik et al., 2018; Woodroffe and Ginsberg, 1998; Yaner, 1988). Researchers continue to discuss what is better: few large protected areas or many small regions, resulting in mixed reviews (Balmford et al., 2019; Burkey, 1989; Collas et al., 2017; Feniuk et al., 2019; Fischer and Lindenmayer, 2002; Helmstedt et al., 2014; Järvinen, 1982; McNeill and Fairweather, 1993; Ovaskainen, 2002; Pickett and Thompson, 1978; Tscharntke et al., 2002). Additionally, migratory species may use scattered locations across a vast landscape, making it difficult to protect habitats of such species (Nandintsetseg et al., 2019; Williams et al., 2012). Therefore, despite our best efforts to keep wildlife in national parks, wildlife refuges, and other protected areas, there is still the need to maintain wildlife-friendly practices in anthropogenic landscapes (Fischer et al., 2008; Goddard et al., 2010; Tscharntke et al., 2002).

In this study, we use the timber rattlesnake, *Crotalus horridus*, as a case study to explore the efficacy of a small nature preserve to maintain a wide-ranging species of concern. Land management practices and the decisions we make on the best ways to protect wildlife are vital to the long-term conservation of wildlife and biodiverse habitats. Here, we quantified and considered the conservation implications of multiple metrics of movement ecology, including daily and seasonal movement patterns, habitat selection, home range size, and site fidelity, in a rural fragmented landscape.

2. Methods

2.1. Study area and species description

This study was conducted within a small 252 ha nature preserve (exact location concealed to protect the rattlesnake population) in central Tennessee from 2012 to 2015. The nature preserve is composed of a mosaic of mixed hardwood forests, old growth fields, redcedar forests (*Juniperus virginiana*), and patches of cedar barrens and rocky glades. A forested limestone ridge with extensive karst fissures transects the study area, which is heavily used by multiple species of snake during winter. The nature preserve is bordered by agricultural land, primarily grazing pastures, and rural housing on all sides. Paved roads surround the study site and in multiple locations are adjacent to or within a few hundred meters of the preserve.

Timber rattlesnakes (*Crotalus horridus*) are large bodied and potentially long-lived (Brown, 2016; Brown et al., 2007) pit-vipers found throughout much of the eastern United States (Powell et al., 2016). In recent decades, the wide distribution of timber rattlesnakes has become sparse and noncontinuous in many regions (Martin et al., 2008) with populations suffering from large declines, primarily due to habitat loss, fragmentation, and increased mortality from roads and human persecution (Brown, 1993; Clark et al., 2010; Martin et al., 2008). Timber rattlesnakes can travel great distances (e.g., mean ± SE = 3514.1 m ± 14.9; range = 537.6 – 10, 432.2 m; Smith, 2013; mean ± SE = 2231.1 m ± 380.7; range = 727 – 7289 m Reinert and Zappalorti, 1988); throughout the warm summer months to reach core areas to forage and search for mates before returning to overwintering sites (Brown, 1992, 1982; Nordberg and Cobb, 2017, 2016). Such movements potentially allow timber rattlesnakes to encounter a variety of habitats, even though they are typically associated with forested or woodland habitats throughout most of their range (Gibson et al., 2008; Reinert, 1984; Reinert and Zappalorti, 1988; Waldron et al., 2006).

2.2. Snake capture and radio telemetry

We captured all rattlesnakes using drift fence arrays around known denning areas or through opportunistic captures throughout the year. We anesthetized each snake for radio transmitter implantation using an isoflurane inhalant delivered through a clear plastic tube. While anesthetized, we collected morphological data (e.g., SVL, tail length, body mass, reproductive status, number of rattles, etc.) and surgically implanted a passive integrated transponder (PIT) tag (AVID Identification Systems, Inc., Norco, CA) for long-term individual recognition and a radio transmitter (SB-2 or SI-2, Holohil Systems, Inc., Ottawa, ON). Implanted devices were placed into the body cavity adjacent and posterior to the stomach following surgical procedures of Reinert and Cundall (1982) and did not exceed 5% of snake body mass. We maintained postoperative snakes in an environmental chamber (30:27 C, day:night cycle) for up to 48 hrs to promote wound healing before release at the site of capture. Rattlesnakes were relocated 2 – 3 times per week to quantify daily and seasonal movement patterns and habitat use using a three-element Yagi antenna and handheld receiver (R-1000, Communications

Specialist, Inc., CA). We recorded snake locations with a handheld GPS unit (GPSMAP 76CSx, Garmin International, Inc., KS).

3. Data analyses

3.1. Movement patterns

We calculated the total distance travelled by each snake by adding the cumulative straight-line distance between successive relocations. In addition, we calculated the furthest extent each snake travelled by calculating the straight-line distance between the furthest point from their denning location. We used linear mixed-effects models (LME; *lme4*; Bates et al., 2015) to identify factors that influenced both total distance travelled and furthest extent distance. We constructed a full model that included reproductive status (male, female, or gravid), and SVL (cm) as fixed effects. Given the repeated nature of our study, we used individual snake ID as a random factor to account for individual variation in our repeated measures design. We conducted model selection using the dredge function in the package MuMIn (Barton, 2019) based on Akaike's information criterion (AICc, corrected for small sample sizes) with the assumption that models with the lowest AICc values had the greatest explanatory power, model fit, and model parsimony (Burnham and Anderson, 2004). We used the package emmeans (Lenth, 2019) to explore post-hoc pairwise comparisons where appropriate. We conducted all statistical analysis within the program R (version 3.5.2, R Core Team, 2018), and examined boxplots and residual plots for normality and homogeneity of variance, and calculated model fit (marginal and conditional R^2 values; Lefcheck, 2016). Statistical significance was assumed to be $P < 0.05$, and all means are presented ± 1 SE.

3.2. Habitat selection

At every rattlesnake telemetry relocation, we classified broad habitat (i.e., old field, mixed hardwood forest, cedar glade and barren, agricultural field, and other) and microhabitat characteristics. In addition, we visually estimated the percent ground vegetation cover within a 1 m^2 area of each rattlesnake location. Similarly, we estimated the percent canopy cover directly over the snake location. We paced out the distances to the nearest habitat edge and also to the nearest log or brush pile. After assessing microhabitat features at a rattlesnake location, we quantified whether rattlesnakes were selecting particular microhabitat characteristics by assessing the microhabitat characteristics of a set of 504 random points within 50 m of a rattlesnake location. To identify random point locations, we selected a random direction (1 – 360 degrees) and distance (1 – 50 m) using a random number generator. We used the next randomly generated direction and distance for the next random point. We compared the proportion of rattlesnake locations in each microhabitat category compared to the distribution of random points in those categories. We used the adehabitatHS R package (Calenge, 2006) with a type II design to calculate Manly selection ratios for each habitat type. Manly selection ratio values close to 1 (or values with 95% confidence intervals overlapping 1) represent random selection, indicating animals were found in that category in proportion to its availability (i.e., no habitat selection). Values greater than 1 (with non-overlapping 95% CIs) indicate a positive selection with animals selecting these categories disproportionately more than their availability. Values less than 1 (with non-overlapping 95% CIs) indicate a negative selection or avoidance, where animals actively avoid particular habitats.

To assess broad habitat characteristics, we created a shapefile using QGIS (QGIS Development Team, 2018) and digitized broad-scale habitat features at the study site using aerial satellite imagery. Broad-scale habitat categories were inspected on foot to ground-truth each category type to ensure correct habitat classification. To test for habitat selection by rattlesnakes, we overlaid our rattlesnake locations via telemetry on top of our study site shapefile and used a spatial join function in the R package *sf* (Pebesma, 2018) to extract the broad-scale habitat for each snake location. This was corroborated with our on-ground habitat assessments. We compared snake locations in each habitat to random points generated throughout the study site. We created 1000 random points using the *st_sample* function and conducted another spatial join, as described above. We compared the proportion of locations in each habitat type compared to the distribution of random points using the adehabitatHS R package (Calenge, 2006) with a type II design to calculate Manly selection ratios for each broad-scale habitat type.

3.3. Home range

We calculated two commonly used metrics of home range estimates, minimum convex polygons (MCPs) and 95% kernel utilization density estimates (KUDs). Both metrics are useful and provide valuable information about the space use of animals. MCPs show extent and total area used while KUDs show areas of core use. In addition, using both methods facilitate comparability among other studies that may have used one or the other metrics. We calculated adjusted KUD estimates as recommended by Row and Blouin-Demers (2006). They highlight that reptile studies generally show inflated KUD estimates due to relatively low relocations and the relatively sedentary lifestyle of many reptiles. The clustering of points in few core areas make it difficult to select an appropriate smoothing factor to create the kernels. Therefore, Row and Blouin-Demers (2006) proposed a technique to adjust the smoothing factors to make 95% KUDs equal the same areas as MCPs. We followed this methodology (described and annotated in Paterson's online workshop [Paterson, 2018]) for our home range estimates using the R package adehabitatHR (Calenge, 2011). In addition, we compared year-to-year home range overlap for individuals that were monitored in multiple years to identify broad-scale and microhabitat site fidelity.

4. Results

We captured a total of 25 timber rattlesnakes (*C. horridus*) for VHF radio transmitter implants (Table 1). We accumulated 1539 rattlesnake relocations in total, from relocations two to three times per week during their active season (April–Oct) in 2012–2015. Rattlesnake relocations ranged from 10 to 86 relocations during the active season depending on the year and fate of each snake. Some individuals were monitored up to four consecutive active seasons (e.g. 158 relocations over 4 years). Male rattlesnakes showed the largest home rages (MCP = 51.3 ha; KUD = 51.5 ha) compared to females (MCP = 46.9 ha; KUD = 47.1 ha) or gravid females (MCP = 45.0 ha; KUD = 46.8 ha). Our top linear mixed-effects models indicated that both reproductive status and SVL (size) were important factors to be included in our models for home range size (for both MCPs and KUDs; Table 3). In both cases, models indicated that larger snakes (greater SVL) showed significantly larger home range sizes ($p < 0.001$ for both KUD and MCP; Table 4). Given we scaled our home range size analyses to match KUD = MCP (see home range analyses above), it was unsurprising that we found the same result when analyzing data for both MCP and KUDs.

Timber rattlesnakes showed to be largely generalists in terms of broad-scale habitat features. However, snakes showed a significant positive selection for cedar glades and barrens, while they used all other broad habitat categories equal to their availability (Table 2). Rattlesnakes avoided completely closed and completely open canopy habitats, exploited low to middle canopy cover (10–50% canopy cover), and used all other canopy categories equal to their availability (Fig. 1). In contrast, snakes avoided low ground vegetation cover (0–20% ground vegetation cover), exploited heavy to medium ground cover (80–90% ground vegetation cover), and used all other ground vegetation cover categories equal to their availability (Fig. 1). In addition, snakes showed a positive association with habitat edges, with snakes selecting locations from 0 to 9 m to a habitat edge more often than their availability. Similarly, snakes chose locations that were close to brush piles or logs more than their availability (0–9 m; Fig. 1).

Through model selection, our linear mixed-effects models indicated that KUD, reproductive status, and SVL were all important predictors of total distance travelled by snakes during their active season (Table 3), however, SVL was the only variable that showed a significant relationship (LME: $F = 5.129$, $P = 0.033$, Table 4), where larger snakes accumulated a greater cumulative distance travelled than smaller snakes (Pearson's correlation: $r^2 = 0.63$). Our top model for furthest extent distance included only SVL, which showed a

Table 1
Summary of timber rattlesnake (*Crotalus horridus*) movement data. Age = adult (A) or subadult (Sub); # Reloc. = number of relocations; MCP (ha) = minimum convex polygon; KUD (ha) = adjusted 95% kernel utilization density estimates (Row and Blouin-Demers, 2006); % KUD outside preserve = the % of core area use that falls outside the protection of the nature preserve; Total dist. = cumulative distance travelled; Furthest extent = greatest straight-line distance from known hibernacula to furthest point.

Year	Snake ID	Sex	Age	SVL (cm)	# Reloc.	MCP (ha)	KUD (ha)	% KUD outside Preserve	Total dist. (m)	Furthest extent (m)
2012	1	M	A	99.0	57	130.9	131.5	70.0	10,019.2	1818.8
	3	F	A	98.5	82	102.8	102.4	54.3	6353.9	1623.3
	4	F	A	112.0	65	83.1	80.7	56.3	8033.3	1868.2
	5	M	A	85.0	79	16.1	16.0	0.9	3740.8	653.0
	6	F	Sub	67.0	86	7.9	8.0	7.9	2515.2	281.3
	7	F	A	91.5	73	33.9	39.3	52.7	6650.6	1324.0
	8	F	A	103.0	75	78.3	80.9	74.3	6699.3	1858.2
2013	1	M	A	108.0	57	195.3	196.7	63.5	7332.4	1786.1
	3	F	A	98.5	14	24.6	22.4	36.3	2422.2	1666.6
	4	F	A	112.5	47	162.6	163.8	77.4	4190.5	1844.2
	5	M	A	88.0	59	27.0	27.4	6.2	5075.9	815.8
	6	F	Sub	69.8	66	26.0	26.8	79.0	3015.9	967.9
	8	F	A	104.0	56	47.2	50.4	83.2	4241.9	1891.5
	10	F	A	103.0	55	21.5	21.2	100.0	1948.7	843.0
	11	F	A	108.0	58	57.4	56.7	82.5	5790.9	1035.7
	13	F	Sub	68.0	33	31.0	31.1	8.7	3154.5	572.9
	14	M	A	55.7	64	10.1	10.2	0.0	1608.7	745.1
	15	F	Sub	68.0	54	9.6	9.9	69.9	2933.7	681.6
	16	F	Sub	67.0	63	7.3	7.3	0.0	1802.2	454.6
	17	M	A	98.2	54	73.3	72.3	11.3	5715.1	1292.9
	18	M	A	93.0	48	22.0	22.0	4.3	4769.7	803.4
	19	F_G	A	92.5	36	1.9	1.9	100.0	635.8	839.7
2014	4	F	A	113.0	21	57.7	55.6	71.0	4387.0	2081.0
	18	M	A	98.7	11	45.1	48.2	11.6	3472.7	1329.8
	20	M	A	72.0	12	97.6	97.1	58.4	3341.6	–
2015	4	F	A	114.0	25	65.0	63.6	45.4	5342.7	1812.4
	11.1	F_G	A	110.5	14	88.0	91.8	27.0	6139.0	1209.4
	17	M	A	108.0	24	50.9	49.5	95.8	3844.5	1935.9
	23	M	Sub	66.0	15	15.9	15.7	26.7	1468.3	385.5
	24	F	Sub	68.5	27	10.8	10.9	0.0	1787.8	364.9
	25	F	A	98.0	27	29.5	29.7	90.7	2481.9	751.4
	26	M	Sub	63.5	14	2.3	2.4	100.0	846.1	690.7
	27	F	A	70.7	30	34.0	33.9	84.5	2947.5	597.6
	28	M	Sub	59.1	15	4.4	4.4	55.5	1059.9	621.9
	29	M	A	87.0	23	27.1	27.8	65.9	3540.4	920.8

Table 2

Habitat selection (Calenge, 2006) of timber rattlesnakes (*Crotalus horridus*) in a fragmented agricultural landscape. Avail. = proportion available for each habitat category in the landscape; Used = the proportion of each habitat used by rattlesnakes; W_i = Manley selection ratio (values above 1 represent positive selection (used disproportionately more than the availability, values below 1 show avoidance (used disproportionately less than availability); and values with 95 CI ranges that include 1 show random selection (used in proportion to availability); SE = standard error; 95 CI = 95% confidence interval; Response = a positive selection (+), negative selection/avoidance (-), or NS = not significant (random selection).

Habitat	Avail.	Used	W_i	SE	95 CI lower	95 CI upper	Response
Cedar barrens & glades	0.049	0.153	3.132	0.744	1.169	5.095	+
Cedar forest	0.070	0.054	0.779	0.278	0.046	1.511	NS
Agriculture pasture	0.128	0.084	0.656	0.255	-0.018	1.329	NS
Mixed hardwood forest	0.659	0.569	0.863	0.094	0.616	1.110	–
Old growth field	0.045	0.115	2.561	0.852	0.313	4.810	+
Other	0.049	0.024	0.499	0.275	-0.226	1.224	NS

Table 3

Model selection results using the dredge function in the R package MuMIn (Barton, 2019) based on Akaike's information criterion (AICc) with the assumption that models with the lowest AICc values had the greatest explanatory power, model fit, and model parsimony (Burnham and Anderson, 2004).

Response	Model terms	Random	df	logLik	AICc	ΔAICc	Weight
Sqrt(Total distance travelled (m))	KUD + Reproductive status + SVL	Snake.ID	7	-125.792	269.9	0.00	0.455
	KUD + Reproductive status	Snake.ID	6	-127.629	270.4	0.48	0.358
	Reproductive status + SVL	Snake.ID	6	-128.432	272.0	2.08	0.160
	KUD	Snake.ID	4	-133.796	277.0	7.08	0.013
	KUD + SVL	Snake.ID	5	-132.540	277.2	7.33	0.012
Log(Furthest extent distance (m))	SVL	Snake.ID	4	-15.258	39.9	0.00	0.962
	Reproductive status + SVL	Snake.ID	6	-15.804	46.7	6.82	0.032
	KUD + SVL	Snake.ID	5	-19.059	50.3	10.36	0.005
	Null	Snake.ID	3	-24.262	55.3	15.43	0.000
	KUD + Reproductive status	Snake.ID	4	-24.254	57.9	17.99	0.000
KUD (ha)	Reproductive status + SVL	Snake.ID	6	-163.943	342.9	0.00	0.987
	Reproductive status	Snake.ID	5	-169.932	351.9	9.05	0.011
	SVL	Snake.ID	4	-172.737	354.8	11.92	0.003
	Null	Snake.ID	3	-178.269	363.3	20.43	0.000
MCP (ha)	Reproductive status + SVL	Snake.ID	6	-163.583	342.2	0.00	0.987
	Reproductive status	Snake.ID	5	-169.551	351.2	9.00	0.011
	SVL	Snake.ID	4	-172.430	354.2	12.03	0.002
	Null	Snake.ID	3	-177.878	362.5	20.36	0.000

Table 4

Results of the top model (LME; Bates et al., 2015) after model selection. Dist. represents the model distribution (G = Gaussian) and R^2 represents the marginal (fixed effects only) and conditional (full model, including random effects) model fit respectively.

Response variable	Terms in top model	Random effect	Dist.	F-value	P-value	R^2
Total distance travelled (m)	KUD	Snake.ID	G	8.680	**0.006**	0.59, 0.59
	Reproductive status			1.231	0.313	
	SVL			5.129	**0.033**	
Furthest extent distance (m)	SVL	Snake.ID	G	38.448	**<0.001**	0.60, 0.85
MCP (ha)	Reproductive status	Snake.ID	G	0.979	0.391	0.35, 0.52
	SVL			14.982	**0.001**	
KUD (ha)	Reproductive status	Snake.ID	G	0.914	0.415	0.35, 0.50
	SVL			14.966	**0.001**	

significant influence on furthest extent distance (Table 4). Again, larger snakes showed a higher tendency to travel further from the overwintering den site than smaller snakes.

Many rattlesnakes showed high site fidelity and year-to-year overlap in home ranges, repeatedly returning to the same core areas year after year (Fig. 2). This was especially true for core foraging and mating areas at the furthest extent of their home range as well as returning to communal hibernacula prior to brumation. Our sample size was too small for statistical tests, but we anecdotally note that smaller snakes were more likely to have lower year-to-year home range overlap than larger snakes (Fig. 2). It appears that larger snakes have established home ranges, whereas younger snakes show more exploration in habitats among years. In some cases, snakes used the same travel corridors in multiple years to navigate through fragmented landscapes. For example, snakes #8 and #10 navigated through a mosaic of agricultural fields via narrow fence and tree rows to avoid open agricultural fields with livestock and heavy machinery (Fig. 3).

We assessed what proportion of snake relocations fell within and outside the boundary of the nature preserve. Despite ample

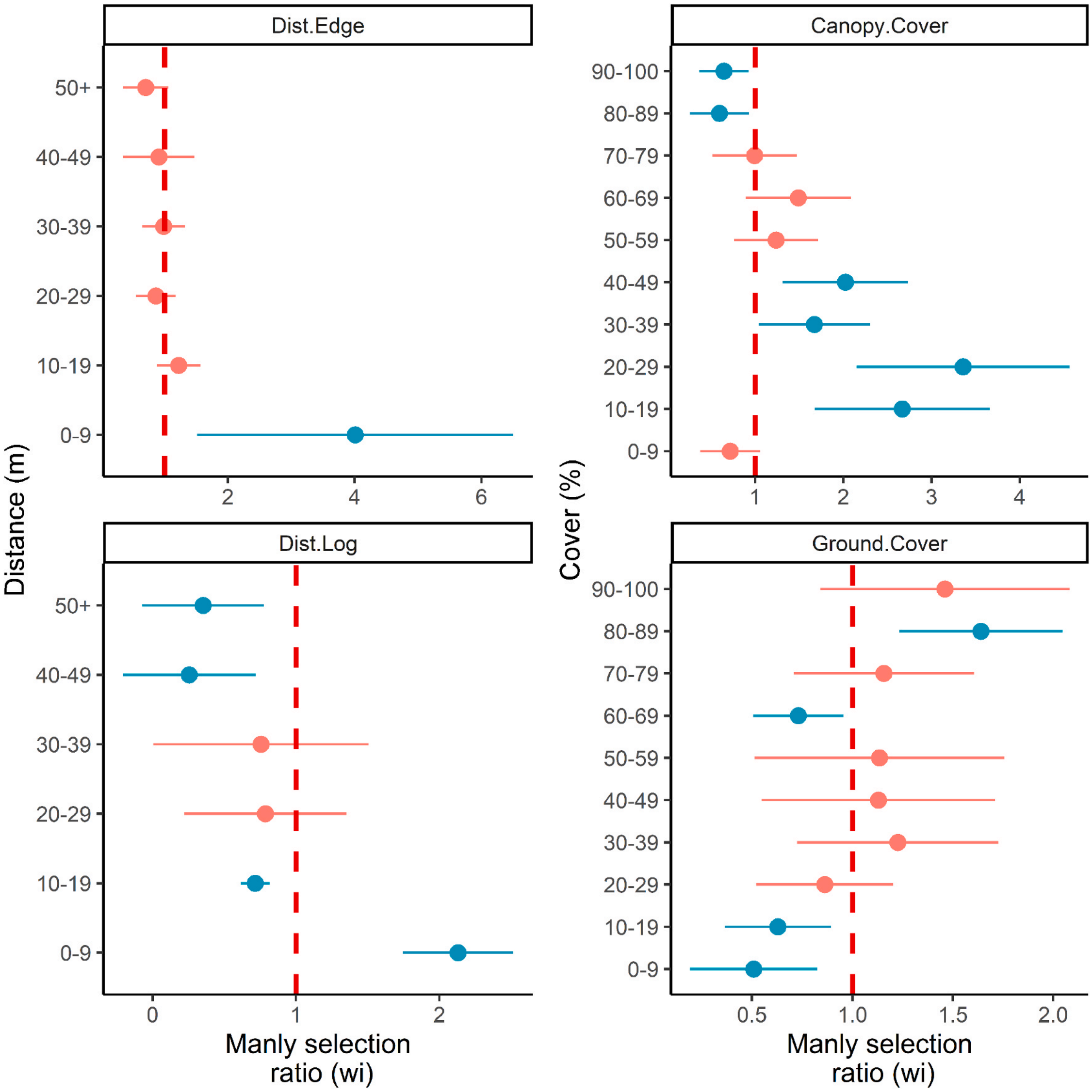

Fig. 1. Microhabitat selection in timber rattlesnakes (*Crotalus horridus*). The y-axis represents binned values of distance (distance to forest edge or to nearest log) or binned percent cover measures (canopy cover or ground vegetation cover). The x-axis represents a measure of Manly selection ratios. Selection values greater than 1 (with non-overlapping confidence intervals [CIs]) represent positive selection (used disproportionately more than their availability), values less than 1 (with non-overlapping CIs) represent avoidance (used disproportionately less than their availability), and values with CIs overlapping 1 indicate random selection. Values that are significantly different from random selection are shown in blue, non-significant terms are shown in red.

suitable habitat within the nature preserve, only 50.7% of all snake relocations were contained within the nature preserve boundary (Fig. 4). Twenty-four of 25 snakes used space both inside and outside the nature preserve. Further, 60.9% (median) of core area use for foraging and mate-searching in adult rattlesnakes fell outside the nature preserve boundary. The preserve does, however, contain important hibernacula for most of the snakes in this study (Nordberg and Cobb, 2017, 2016). All of our telemetered snakes except one (#10) overwintered within the preserve boundaries; this individual hibernated nearby the preserve border and spent time on and off of the preserve during its activity season.

4.1. *Known mortality*

Fortunately, we did not observe substantial mortality during the course of our study. One adult male was killed on a boundary paved road in the third year of monitoring, one adult female was killed by heavy farm equipment along a fence row during the second year of monitoring, one subadult individual was predated by an adult eastern kingsnake (*Lampropeltis getula*) and two snakes had unknown fates but were presumably associated with overwintering as they did not emerge the following spring.

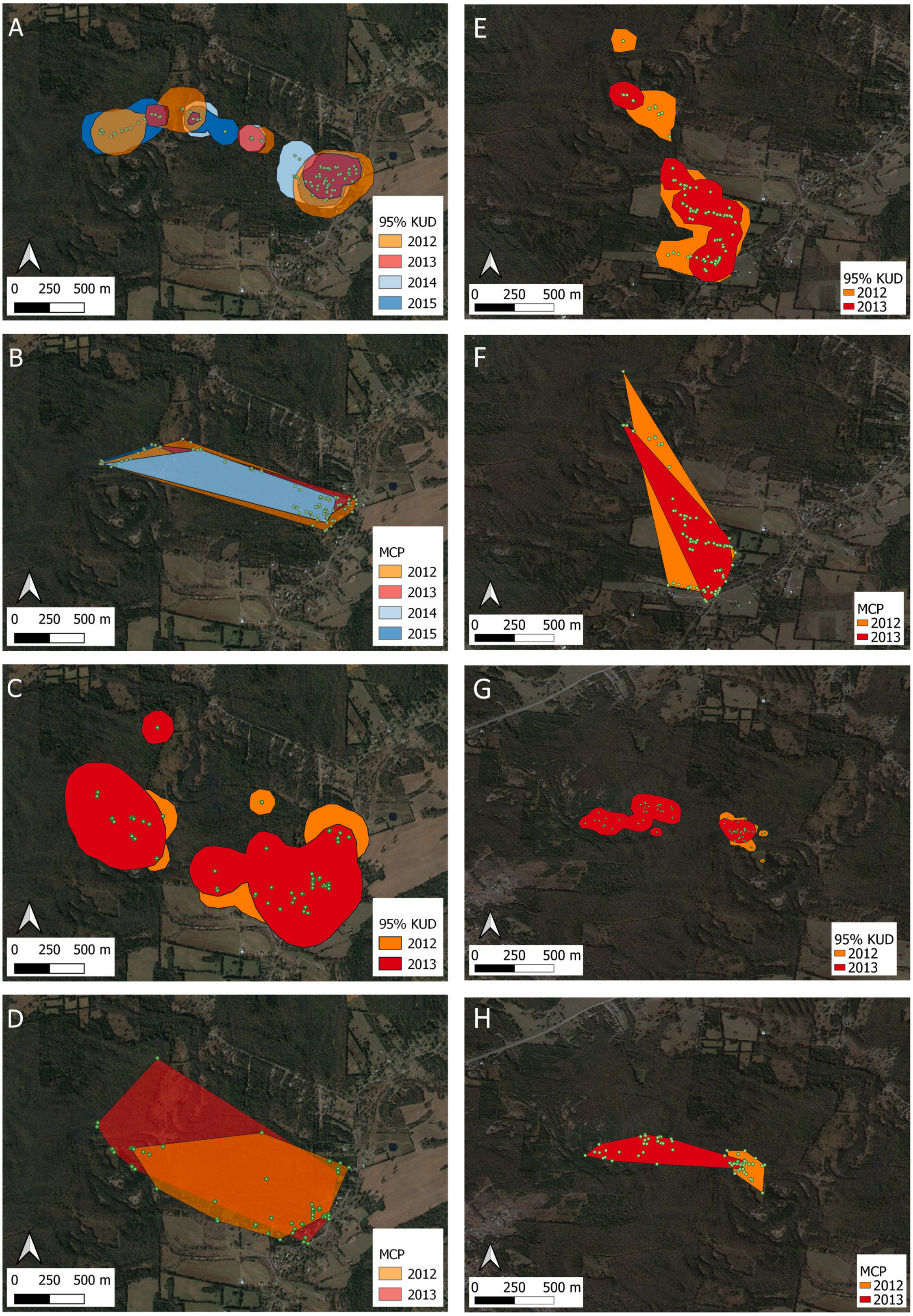

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Fig. 2. Adult timber rattlesnakes (*Crotalus horridus*) showed high site fidelity, returning to the same locations year after year (A and B = rattlesnake #4; C and D = rattlesnake #1; E and F = rattlesnake #8). Subadult rattlesnakes showed more variability in their active season movement patterns, however, overwintering site fidelity remained high (G and H = rattlesnake #6).

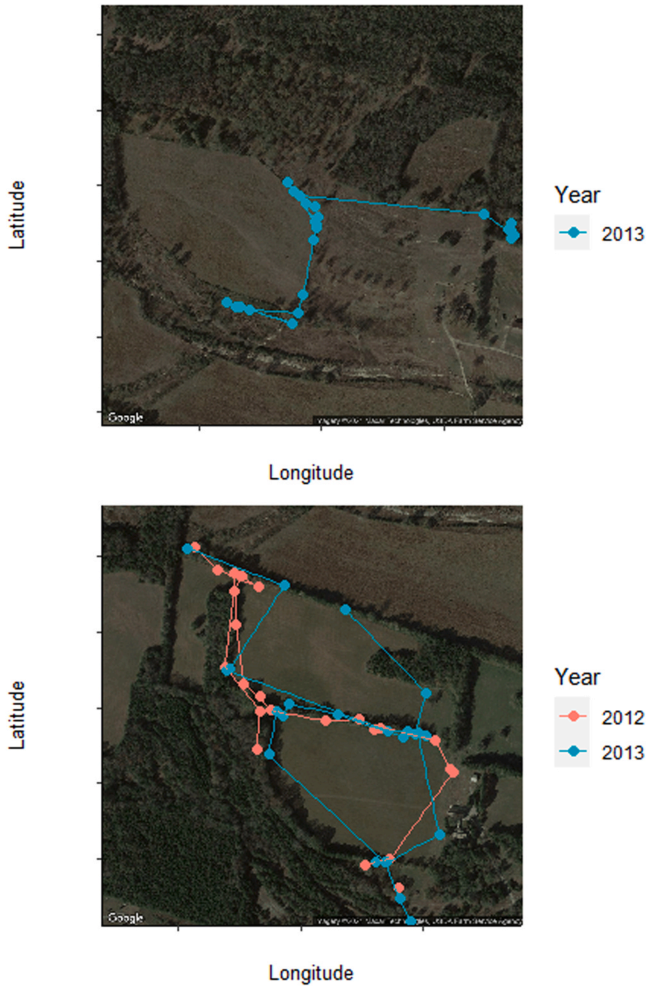

Fig. 3. Examples of two different timber rattlesnakes using tree rows to navigate through agricultural pasture. The snake on the bottom panel used the same travel corridor in multiple years. Latitude and longitude values are withheld to protect the site location.

5. Discussion

Timber rattlesnakes are large-ranging snakes that use a variety of habitat types (Brown et al., 1982; Reinert, 1984; Reinert and Zappalorti, 1988; Waldron et al., 2006; Wittenberg, 2012). They tend to be habitat generalists at a broad level, using all habitat categories equal to their availability with the exception of cedar glades and barrens. However, in terms of microhabitat use, snakes showed clear patterns of selection in multiple categories (Reinert and Zappalorti, 1988). Our results indicated that snakes chose microhabitat locations that provided an open canopy, which may increase solar radiation to the forest floor, but also have dense ground vegetation cover for shelter and reduced detection (Reinert et al., 2011; Waldron et al., 2008). These conditions may be amplified around habitat edges where dense ground vegetation can accumulate even in the presence of high canopy cover. Further, habitat edges may also support high populations of small mammalian prey items, including grey squirrels (Bennett et al., 1994; Dondina et al., 2016). Timber rattlesnakes showed high site fidelity, returning to the same active season locations and utilized the same hibernacula sites across multiple years (Nordberg and Cobb, 2017, 2016). This highlights the importance of maintaining those microhabitats, as they represent core areas of use for rattlesnakes. A worrying observation was that only 50.7% of all rattlesnake locations were found within the property boundary of the nature preserve. While nature preserves protect vital habitat for many resident species, smaller preserves may not be large enough to protect all the habitat used by wide-ranging residents. These problems are prevalent for large-ranging animals, such as timber rattlesnakes.

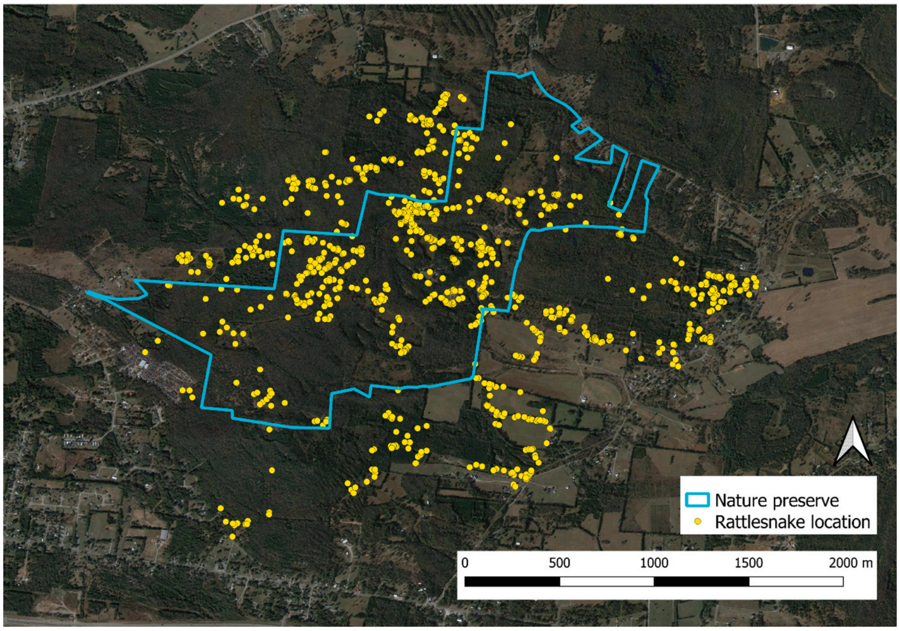

Fig. 4. Small nature preserves (e.g. 252 ha.) do not adequately support all habitat for large ranging snakes. A total of 49% of all rattlesnake relocations (points) fall outside the nature preserve boundary (25 snakes over 3 years).

Nature preserves, national and state parks, wildlife management areas, and other protected areas are designed to retain essential habitat requisite to flora and fauna in addition to providing recreational areas for people. In many cases, these protected areas support healthy populations of many plants and animals (Götmark and Thorell, 2003; Schwartz and van Mantgem, 1997), however, land-sparing preservation tactics have their own set of limitations. While land-sparing can be effective, national parks and other protected areas only make up 12% of land area in the United States (UNEP-WCMC, 2020). In addition, the efficacy of each protected area is highly dependent on the mobility of target species. For animals that do not exhibit large movements or migratory patterns, small, protected areas may adequately protect and support biodiversity (Fischer and Lindenmayer, 2002; Lindenmayer, 2019; Zuidema et al., 1996). However, acquiring enough land to encompass the entire home range of large-ranging species can be costly and in some cases unmanageable (Nandintsetseg et al., 2019; Williams et al., 2012). In addition, animals that live near the periphery of a protected area will still likely venture outside the boundary area, leaving them vulnerable to additional threats such as roads, domestic animals, exposure, or human persecution.

We viewed our study site as a relatively small protected area (252 ha.), however, it is actually reasonably large when compared to all other protected areas across the timber rattlesnake's range. We identified 159,108 protected areas throughout the eastern and midwestern United States, which included national parks, wildlife management areas, and residential protected areas (U.S. Geological Survey (USGS) Gap Analysis Project (GAP), 2020). While some protected areas are extremely large (e.g., Mark Twain National Forest: 609,760 ha.), we found the mean protected area size was similar to our study site (mean: 224 ha.; median = 4 ha.; standard error: 12.7 ha.). We do not intend to diminish the value of large protected areas, we simply aim to highlight the importance of 'small' protected areas as important biodiversity value, especially in fragmented landscapes. We suspect that many people view large national parks as the standard size to be useful protected areas for wildlife conservation, however, these large parks represent the minority, and are greatly outnumbered by smaller nature preserves and protected areas. Mosaics of 'small' protected areas can support many species, especially if travel corridors, habitat patches, and connectivity remain (Burkey, 1989; Fischer and Lindenmayer, 2002).

Conservation tactics, such as retaining habitat patches and travel corridors should add value to the ideas of land-sharing for private land owners. Given the area discrepancy between protected and privately owned land, if we can educate private landowners to maintain ecologically friendly properties, this may have larger conservation returns than scattered protected areas (Neilly et al., 2016, 2017; Billaud et al., 2020). Many animals can maintain healthy populations in peri-urban environments given they have access to particular habitat features. For example, patchy habitat features such as remnant vegetation, tree rows, or linear vegetation corridors can provide connectivity between fragmented habitats and facilitate gene flow among populations (Dondina et al., 2016; Staley et al., 2016).

Habitat fragmentation is one of the largest causes of species declines worldwide (Fahrig, 2003; Fischer and Lindenmayer, 2007). However, many species have been able to persist in highly fragmented habitats by using remaining habitat features (Colding et al., 2009; Harvey et al., 2004; Manning et al., 2006). In our study, timber rattlesnakes spent a large proportion of their time travelling outside the nature preserve: many survived by using travel corridors, remnant tree patches, and fence rows which joined together fragmented woodland patches. Habitat used by snakes outside the nature preserve was largely patchy woodland, rural housing properties, and agricultural land. Navigating through fields with livestock, farming equipment, roads, and rural properties presents many challenges for snakes, including human persecution (Brown, 1993; Martin et al., 2008). In addition to unwarranted persecution from humans or livestock, snakes seeking shelter in agricultural fields may be run over or killed by agricultural equipment or machinery while cultivating fields or crops. Our study indicated that snakes often avoided travelling directly through potentially dangerous habitats, such as agricultural fields, and alternatively used remnant vegetation patches as travel corridors. These remnant habitat patches were essential for rattlesnakes to navigate through highly fragmented habitats to reach core breeding and foraging areas. Snakes in our study showed high selectivity for microhabitats with dense ground cover and/or moderate canopy cover which offer thermal buffering and concealment. Such conditions allowed for snakes to move throughout the landscape with minimal detection from predators and offer thermoregulatory and foraging opportunities. Especially in fragmented landscapes, these habitat buffers increase connectivity for many species (Burel, 1996; Dondina et al., 2016; Reading and Jofré, 2009) and the connectivity they provide can often sustain populations even in fragmented habitats. In addition, grey squirrels and small rodents, which are primary prey items for timber rattlesnakes, are often found along fence and tree rows in fragmented landscapes (Clark, 2002; Stevenson et al., 2013).

Timber rattlesnakes in this region show high site fidelity not only in terms of year-to-year home range overlap, but also in their microhabitat selection, similar to that described in Sealy (2002). Given that many snakes already travel through highly fragmented areas, including navigating along narrow fence rows and habitat patches to avoid open agricultural paddocks, the behavioral drive to return to specific sites is strong in this species. Therefore, it seems unlikely that these snakes will alter their home range in response to further diminished habitat suitability. Rattlesnakes in this population are already foraging around rural houses, barns, and in close proximity to roads and other anthropogenic structures. In addition, barriers such as roads do not seem to physically stop snakes from attempting to cross them; at least one snake from our study was killed while crossing the road. Our data suggests that larger snakes travelled larger distances and migrated further away from the nature preserve than smaller snakes. This makes larger individuals (e.g. reproductive adults) more at risk of encountering roads, farm equipment, or other anthropogenic sources of mortality. A continual loss of large reproductive adults will ultimately lead to population declines given the slow maturity of this species (Brown, 2016; Martin, 2001, 1993). Given that roads directly border the entire study site, we were surprised that we did not observe more road mortality. Interestingly, none of the snakes we monitored via telemetry successfully crossed the boundary road, despite a few individuals being located within a few meters of the road. Perhaps some snakes in this population do avoid crossing roads, which while reducing mortality, could lead to genetic bottlenecks and limit dispersal (Clark et al., 2011, 2010). The drive to return to specific sites may be stronger than the drive to avoid unsafe areas by changing their home range (Lomas et al., 2019; MacGowan et al., 2017; Reinert et al., 2011). Furthermore, these snakes have a long history of returning to communal dens at the end of every season to brumate during the colder months (Nordberg and Cobb, 2017, 2016).

Timber rattlesnakes are listed as a species of concern, threatened, or endangered across large parts of their range in the eastern United States (Brown, 1993; Powell et al., 2016). They are particularly vulnerable to habitat loss, given the large areas they use throughout the year, as demonstrated by this and other studies (Brown et al., 2007; Clark et al., 2011, 2010; Reinert and Zappalorti, 1988; Sealy, 2002; Waldron et al., 2013, 2006). In addition, rattlesnakes are some of the most persecuted animals, with thousands of snakes being collected or killed for rattlesnake round-ups (Means, 2009; Weir, 1992), or because people do not want venomous snakes around their property. The ever-growing human population and expanding urban sprawl continue to put severe pressure on wildlands and undisturbed habitat for rattlesnakes across the United States. While many wildlife species are adaptable and can use and thrive in fragmented landscapes (Durner and Gates, 1993; Kjoss and Litvaitis, 2001; Mitrovich et al., 2009; Nordberg and Schwarzkopf, 2019), this increased pressure often leads to higher mortality as wildlife have greater encounter rates with roads, anthropogenic equipment, and people. Small isolated populations, such as the rattlesnake population described in our study, have persisted in recent years despite major modification of their habitat, but how long can this species survive in such an altered landscape with ever-growing risks and ever-shrinking habitat? While we acknowledge that our study may be limited in geographic scale, many small nature preserves are surrounded by rural or even more industrial landscapes, resulting in similar problems as the timber rattlesnakes described here. In addition, a majority of protected areas are similar in size, if not smaller than our site, indicating the importance of species and habitat management at this scale. Maintaining a landscape with travel corridors, remnant patches of suitable vegetation, and the protection of key habitat features, such as hibernacula, are vital to sustain large-ranging species in fragmented landscapes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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