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THE SPATIAL ECOLOGY OF THE SOUTHERN COPPERHEAD
IN A FRAGMENTED AND NON-FRAGMENTED HABITAT

By

Megan Veronica Novak

Submitted in Partial Fulfillment of the
Requirements for the Degree of Master of Science in
Coastal Marine and Wetland Studies in the
School of Coastal and Marine Systems Science
Coastal Carolina University

2017

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**The spatial ecology of the southern copperhead
in a fragmented and non-fragmented habitat**

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ABSTRACT

Habitat fragmentation may alter the spatial ecology of organisms inhabiting the fragmented landscape by limiting the area of habitat available and altering microhabitat features. I quantified and compared movement of southern copperheads (*Agkistrodon contortrix contortrix*) in a fragmented and non-fragmented habitat to determine the effects habitat fragmentation has on the movement of the southern copperhead. Effective distance moved by each individual was measured by the use of thread bobbins attached via medical tape to the posterior quarter of the snake. Straight-line distance moved and occupied area were calculated with the GPS coordinates recorded at each snake sighting. Straight-line distance moved and occupied area did not differ between fragmented and non-fragmented habitats. However, season-specific effective distance moved differed between fragmented and non-fragmented habitats. In fragmented habitats, effective distance moved by individual snakes increased from summer to autumn, whereas, it decreased in non-fragmented habitats. Increased snake movement from summer to autumn in fragmented habitats may have been the result of coinciding increased human activity during this time. Increased exposure of snakes to humans through direct encounters such as outdoor recreational activities and indirect encounters through increased vibrations from vehicles, lawn mowers, and foot traffic may have

disrupted endogenous movement behaviors and prompted an agitated movement pattern. I also quantified microhabitat use by the snakes between the fragmented and non-fragmented habitat to determine if microhabitat suitability was influenced by fragmentation. Tracked snakes were located and microhabitat use was measured within a 1m² quadrat was placed around the snake capture location. Background microhabitats were randomly selected and microhabitat characteristics were quantified. Background sites were assessed as microhabitat available to the snakes but not chosen. Microhabitat characteristics were measured by quantifying the number of trees, woody vegetation stems, herbaceous vegetation stems, percent grass cover, and percent canopy cover. Microhabitat features were similar between the fragmented and non-fragmented environments; however, the number of herbaceous vegetation stems and percent canopy cover were the only model terms that were associated with locations where snakes were observed (BIC = 468, $\omega_i = 0.47$). It is likely *A. contortrix* can persist in a variety of habitats in the southeast because their preferred microhabitat features are widely distributed and common in both fragmented and non-fragmented environments.

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CHAPTER I: DISSIMILAR SPATIAL ECOLOGIES OF THE SOUTHERN COPPERHEAD
(*AGKISTRODON CONTORTRIX CONTORTRIX*) BETWEEN A FRAGMENTED AND NON-
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INTRODUCTION

Spatial ecology of organisms is influenced by habitat structure, environmental conditions (e.g., temperature and moisture), spatial and temporal distribution of resources (e.g., food availability), mates, reproductive habitats, and competition (e.g. Gregory et al. 1987, Webb and Shine 1998, Gibbons and Semlitsch 2001, Lillywhite 2001, Corey and Doody 2010, Howze and Smith 2015). Resources that vary both temporally and spatially may require individuals to utilize large areas; however, locations with relatively abundant and stable resources allow individuals to use a comparatively smaller proportion of available space to fulfill physiological demands (Corey and Doody 2010). When essential habitat for an organism is destroyed or fragmented, the composition of that habitat and resource availability within that habitat are disturbed. Habitat fragmentation consequently may influence the spatial ecology of the organisms inhabiting that landscape.

Habitat fragmentation is defined as the breaking apart of formerly continuous habitat or disconnection between habitat types (Fahrig 2003, Row et al. 2012). Rapid increase in human population size and associated urban sprawl (Wilson 1986, Moreno-Rueda and Pizarro 2007, Buuveibaatar et al. 2016, Gagné et al. 2016) result in fragmentation of contiguous habitats due to construction of roads and development of land for agricultural, suburban, and urban uses (Germaine and Wakeling 2001). Fragmented habitat patches are separated by areas of highly modified, potentially unsuitable habitats, which may function as barriers to dispersal (Ricketts 2001, Shepard et al. 2008). Consequences of habitat fragmentation on long term population viability varies among taxa, distance between habitat patches, and habitat patch size. For some species, habitat fragmentation reduces long term population viability (Flather and Bevers

2002, Cattarino et al. 2016). For example, populations of white spotted char (*Salvelinus leucomaenis*), a salmonid fish, existing within fragmented habitats are unlikely to have long-term viability (Morita and Yokota 2002). Habitat fragmentation has also resulted in a decrease in gene flow for a variety of species (Dileo et al. 2010, Wang et al. 2016). Other taxa are either not hindered by habitat barriers (Wiegand et al. 2005) or may benefit from increased edge habitat that fragmentation provides. In addition to the physical effects of fragmentation on dispersal, fragmentation is also associated with an overall increase in human activity across the landscape (Germaine and Wakeling 2001) and an increased probability of human-animal encounters. Animals may perceive human presences and disturbances just as they perceive threats of predation (Walther 1969). Because habitat selection is a trade-off between predation risk and access to resources (Frid and Dill 2002), proximity to humans may influence animal movement and habitat use in addition to the direct effects of habitat fragmentation.

The objectives of this study were to quantify and compare movement patterns and habitat use of the southern copperhead (*Agkistrodon contortrix contortrix*) in a fragmented suburban habitat and non-fragmented habitat in South Carolina, USA. I chose the southern copperhead as a focal species to study the consequences of habitat fragmentation on spatial ecology because the southern copperhead is a relatively abundant habitat generalist occurring in woodlands, bottomlands, edges of wetlands, and farmlands ranging from Texas to Connecticut, and are also capable of persisting in suburban environments (Bachleda 2001), making them the species of interest in this study as they are able persevere in both fragmented and non-fragmented habitats. The copperhead forages in leaf litter and uses fallen branches or logs as refuge material (Bachleda 2001). Though the spatial ecology of the northern copperhead (*Agkistrodon*

contortrix mokasen) have been studied by Smith et al. (2009), relatively little is known about the spatial ecology of the southern copperhead (Sutton et al. 2017).

To study the spatial ecology of southern copperheads, I tracked individuals every 48 hours, noted habitat use (i.e., whether the snakes were in the forest edge, core, or open), and area occupied over the course of the spring, summer, and autumn activity seasons. I hypothesized that (1) copperheads in non-fragmented habitats move longer distances than copperheads in fragmented habitats, and (2) copperheads in non-fragmented habitats have larger occupied areas than those in fragmented habitats.

METHODS

Field Sites

Fieldwork was conducted from May 2016 to October 2016 at a site with limited fragmentation and one fragmented site in Conway, Horry County, South Carolina (Figure 1). The non-fragmented site was in the Waccamaw National Wildlife Refuge (WNWR, 33° 47' 7.32" N, -79° 1' 59.59" W), and consisted of continuous southeastern pine/hardwood forest and swamp bottomland bisected by foot trails and a single dirt road (approximately 27.74 ha). The fragmented site, was located on the campus of Coastal Carolina University (CCU, 33° 47' 42" N, -79° 0' 43.2" W). Habitat within the fragmented site consisted of relatively small patches of mixed pine and hardwood forest (average patch size of 1.66 ha) resulting from secondary succession that was separated by buildings, parking lots, open athletic fields, and paved roads. The two study sites were about 2.25 km apart (linear distance).

Study species and species collection

Southern copperheads ($N_{CCU} = 21$ females, 1 male, and 27 juveniles; $N_{WNWR} = 12$ females, 8 males, 5 juveniles; hereafter referred to as copperhead), were located by

active searching from (0700 h to 2200 h; Table 1), and captured using Gentle Giant™ snake tongs (Midwest Tongs, Greenwood, MO). After capture, snakes were placed into a 5-gallon plastic bucket until processed for attachment of thread bobbins (described below). Snakes were weighed (nearest 0.1 g) using a PESOLA 42500 medio-line metric spring scale (2500 g, Schindellegi, Switzerland), sexed by external palpation, and induced to crawl into a clear, plastic restraining tube (Midwest Tongs, Greenwood, MO) for bobbin attachment. Sex of snakes was confirmed independently by two people.

Quantifying movement

The secretive nature of copperheads makes studies of their movement patterns and habitat use difficult to compare to more active and conspicuous taxa. Radio telemetry is an effective and commonly used approach for studying the long-term activity and movement patterns of free-ranging snakes in the field, though it can be expensive and requires anesthetizing snakes to surgically implant the transmitter. In lieu of radio transmitters, I attached thread bobbins to snakes, and tracked the thread that pulled free from the thread bobbin during movement of snakes between sampling periods. Thread bobbins have been successfully used for spatial movement quantifications on amphibians, chelonians, small mammals, and reptiles (Dole 1965, Wilson 1994, Vieira and Cunha 2002, Toledo et al. 2005, Tozetti and Toledo 2005, Tozetti and Martins 2007). Using thread bobbins for investigations of animal movement is non-invasive, considerably cheaper than radio telemetry, and provides more fine scale movement information compared to telemetry. Unless animals are tracked continuously, detections using radio telemetry only provide information on straight-line distance moved between detection periods; whereas, the release of thread by a moving snake allowed me to follow the path of movement between time periods that each snake was located. Following the procedure of Wiley et al. (2011), prior to attachment, thread bobbins

(0.00625 lb, <1% of the average mature snake body weight, Imperial Threads Inc., Northbrook, IL) were loosely wrapped with plastic saran wrap with a hole at one end to allow the thread to pull freely as the snake moved (Tozetti and Martins 2007). Bobbins were then gently secured to the posterior quarter of the snake using 3M Transpore™ medical tape (3M, St. Paul, MN, 1 in x 10 yd). The free end of the thread bobbin was tied to a stake in the ground, which allowed the string to pay out freely as the snake moved.

Following the attachment of thread bobbins, copperheads were released at the site of capture and thereafter monitored every other day during either the morning (0700 – 1100 h), afternoon (1200 – 1600 h), or evening (1800 – 2100 h). Survey times for the fragmented and non-fragmented sites alternated each day to ensure that each site was regularly visited at each time period. Snakes were re-located by following the trail of thread left by the bobbin from the location the snake was last observed. When a snake was re-located, longitude and latitude were recorded using a handheld GPS device with an accuracy of ± 3 m (GPSmap 62s, Garmin International Inc., Olathe, KS) and habitat location (e.g. forest edge, core, or open) was recorded for each individual.

Movements of copperheads over each 48 h monitoring period were measured using two approaches: (1) Effective distance moved (EDM), and (2) straight-line distance moved (SLD) between snake sightings. Effective distance moved was determined by measuring the length of string collected between two consecutive capture points. Straight-line distance was measured for each individual with more than two captures (adults and juveniles), whereas EDMs were measured for adults only as juveniles were too small to successfully carry the thread bobbins. Occupied area (m^2) for each snake was assessed by creating convex hull polygons in ArcMAP (ArcGIS Desktop: Release 10.3, Environmental Systems Research Institute, Redlands, CA) generated from longitude, latitude observations of each relocated snake. Snakes of all reproductive

stages were included in the occupied area analysis so long as they had at least three observations to allow for creation of a polygon ($n=28$).

Statistical analyses

Seasons were broken up based upon snake activity (measured by frequency of snake occurrences) rather than the conventional equinox and solstice dates, where Spring was considered May 10 – June 25 (average snake observations = 1.26/day), Summer was defined as June 26 – August 18 (average snake observations = 3.11/day), and Autumn was from August 19 to the end of the field season (October 5) where the average snake observation was 1.52/day. The field season ended on October 5, 2016 due to a hurricane occurrence which prevented access to both sites for several weeks. All statistical analyses were completed in R (R Core Team 2016). General linear mixed models with likelihood ratio tests were used to determine if EDM, SLD, or occupied area differed as a function of macrohabitat (CCU and WNWR), season, or the interaction between the two fixed effects, with snake ID incorporated as a random factor (lme4 R package; Bates et al. 2015). The models were fit using a maximum likelihood procedure rather than restricted maximum likelihood procedure, as the restricted maximum likelihood does not provide valid likelihood-ratio tests. A chi-square test of independence was used to see if there was a habitat location (forest edge, core, or open) preference between the two macrohabitats. To further analyze the difference in habitat location use within the two study sites, two chi-square goodness of fit tests were conducted, one for habitat location use at CCU and a second for habitat location use at WNWR. (lme4 R package; Bates et al. 2015, effects R package; Fox 2003). Individual snakes were sampled more than once in different habitat locations, therefore violating the assumption of independence of the chi-square test. To account for this, 1000 bootstrap samples were generated from the 291 snake observations. Within each bootstrap replicate, a

random observation for each individual snake was selected. Using the bootstrap samples, we conducted chi-square tests and measured the association between habitat location and macrohabitat with Cramer's V. A bootstrap confidence interval for Cramer's V was used to determine if macrohabitat type (fragmented/non-fragmented) influenced the frequency of copperhead microhabitat use (forest edge, core, open). A mean Cramer's V between 0.30 and 0.35 would indicate a strong relationship between macrohabitat and frequency of copperhead microhabitat use. To determine which habitat locations were used within each macrohabitat, three logistic models were tested to achieve each combination of habitat locations. Data are reported as mean \pm CI unless otherwise noted, and probability values less than 0.05 were considered significant.

RESULTS

A total of 74 individuals were actively caught and 291 observations were recorded. Any results from juveniles were removed from the distance dataset (effective distance moved or straight-line distance) as they were unable to move freely with the thread bobbin attached to them. After removing juveniles, we had 42 snakes and 246 observations. Macrohabitat ($p = 0.108$, $R^2 = 0.026$) and season ($p = 0.213$, $R^2 = 0.027$) did not influence either EDM or SLD. However, there was a significant interactive effect of macrohabitat and season on EDM ($p = 0.028$, $R^2 = 0.065$; Tables 2 and 3, Figure 2). Macrohabitat ($p = 0.651$, $R^2 = 0.001$) and season ($p = 0.878$, $R^2 = 0.002$) did not have a significant effect on SLD; however, there was a trend towards reduced activity at the non-fragmented habitat from summer to autumn ($p=0.500$, $R^2=0.005$, Tables 4 and 5, Figure 3). Similarly, there was a trend toward larger occupied area at the non-fragmented site, however overall variation in occupied area did not differ between the

fragmented and non-fragmented habitats (occupied area_{frag} 1037.8 ± 312.7 m²; occupied area_{nonfrag} 2310.9 ± 722.3 m²; p=0.160, R²=0.074).

Cramer's V indicated a strong relationship between habitat location (forest core, edge, open) and macrohabitat (fragmented or non-fragmented study site [$\mu=0.34$]; Figure 4). Results from logistic regression models indicated that edge habitat was used more frequently than core habitat at the fragmented site (Table 6). In contrast, there was not a strong preference between edge (46%) and core (54%) habitat at the non-fragmented site. In both fragmented and non-fragmented habitats, edge and core were used more frequently than open habitat. Overall, snakes used open habitat less $\leq 12\%$ of the time.

DISCUSSION

The movement patterns of the southern copperhead were found to be influenced by fragmentation temporally, but this effect was observed only during the transition from summer to autumn at CCU. Similar to my findings, Tozetti and Martins (2007) showed that the SLD traveled by the South American rattlesnake (*Crotalus durissus*), measured using radio telemetry, was less than that of the EDM measured using thread bobbins. Because SLD does not account for the meandering movement patterns of snakes in the environment, SLD likely underestimates both total distance traveled as well as home range size.

The underlying reason for the difference in EDM as a function of season and macrohabitat between the sites is unclear; however, three factors may be responsible for these observations. First, the increased movement in the fragmented site could be the result of seasonal restlessness. Seasonal restlessness can be triggered by migration,

hibernation, and reproduction; though the onset of seasonal restlessness can also be caused by low-quality resources (Ortolani et al. 2008). For example, captive migratory birds exhibit increased activity approaching and during the time that their wild counterparts would migrate (Gwinner 1986, Eikenaar et al. 2014). Similarly, in mammals, Soay sheep (*Ovis aries*) show evidence of circannual rhythms generated by a pituitary mechanism that allows them to adjust to seasonal photoperiodic changes (Lincoln et al. 2006). Consequently, the increase in movement from summer to autumn by copperheads at the fragmented site may be due to seasonal restlessness as the snakes prepare for winter activity. However, increased movement behavior was not observed in snakes from the non-fragmented environment; therefore, it seems unlikely that the increased movement at the fragmented site is due to seasonal restlessness.

Alternatively, the increased activity in the individuals at the fragmented site from summer to autumn may be due to resource differences between the two study sites (e.g. habitat structure, food availability, temperature). Low quality resources increased activity in parasitoid wasps (*Nasonia vitripennis*; King and Ellison 2006), wolf spiders (*Schizocosa ocreata*; Persons and Uetz 1997), and the omnivorous flower bug (*Orius sauteri*; Nakashima and Hirose 2003). Structural habitat differed between sites (unpublished data); however, we did not specifically assess resource quality at the fragmented and non-fragmented sites. Finally, the increased movement behaviors observed from snakes in the fragmented site may be due to changes in human presence and activity from summer to autumn. The fragmented site, located on the campus of Coastal Carolina University, experiences large fluctuations in human population throughout the year. For example, the campus population increased from 5,101 individuals in the summer of 2016 to 10,479 at the beginning of the fall semester in August. Copperheads on the CCU campus would therefore likely experience increased exposure to humans and associated activity. Direct and indirect exposure of wildlife to humans has been

shown to alter behavioral patterns in a variety of animal taxa (e.g., Stalmaster and Newman 1978, Burger 1981, Sutherland and Crockford 1993, Gander and Ingold 1997, Kerr et al. 2004, Green and Geise 2004). For example, presence of humans hiking, jogging, and biking resulted in the movement of male alpine chamois (*Rupicapra r. rupicapra*) for distances ranging from 43-250 m away from the disturbance location (Gander and Ingold 1997). The distance moved changed based on the time of day and activity (hiking, jogging, and biking); however, all activities resulted in fewer chamois sojourning in the study areas. Bald eagles (*Haliaeetus leucocephalus*) also adjusted their movement behavior when overwintering locations were subjected to simulated human disturbances (e.g., approachment toward an eagle by foot under a vegetation canopy, on a riverbank, and in open meadows). The eagles removed themselves from the disturbed locations by a range of 25-300 m (Stalmaster and Newman 1976). Stride frequency of the Australian skink (*Tiliqua rugosa*) increased when the lizards observed humans at a distance of 1-3 m and after handling (Kerr et al. 2004). Copperheads are exposed to humans at the fragmented site on the campus of CCU through direct encounters such as outdoor recreational activities and indirectly through increased vibrations from vehicles, lawn mowers, and foot traffic. Although I did not directly measure human activity, it is plausible that the increased EDM exhibited by copperheads in the fragmented study site is most likely due to agitated behavior caused by exposure to humans, or a general disturbance due to overall increased levels of activity in their environment, rather than the first two proposed factors (i.e., seasonal restlessness and a difference in resources between the two study sites).

My study provided evidence that along with distance moved, occupied area did not significantly differ between the fragmented and non-fragmented habitats, which is uncommon in the literature. Fragmentation has been shown to create limitations on

animal dispersal (Debinski and Holt 2000), and some studies have shown fragmentation to reduce movement rates and distances moved in several small mammals (Diffendorfer et al. 1985ab, Ims et al. 1993, Wolff et al. 1997). However, shape of the habitat patch as well as location within the patches (forest edge versus core) have also been shown to effect dispersion and movement (Harper et al. 1993, Bowers et al. 1995). For example, adult voles inhabiting edge habitat within a fragmented patch have larger home ranges than those within the core of the patch (Bowers et al. 1995). Our data and others suggest that edge effect can have an inverse effect on spatial behavior that what is typically generalized for fragmented habitats. The copperheads at CCU preferred the edge over core and open locations. It is likely the snakes at CCU preferred the edge habitat because of the thermoregulatory opportunities (Weatherhead and Charland 1985, Ackley et al. 2015), as well as the fact that there is a larger edge to core ratio at the fragmented site than the non-fragmented site. Although thermoregulation was not a focus of this study, other squamate species inhabiting fragmented environments have shown preferences for edge habitat as well, and it was commonly noted to be due to the thermoregulatory benefits (Weatherhead and Charland 1985, Durner and Gates 1993, Blouin-Demers and Weatherhead 2001). Open habitat was never preferred to forest core or edge habitat by the copperheads. It is likely that the snakes preferred edge and core habitats due to the cover from predators provided by the vegetation (Fitch 1999, Andrews and Gibbons 2005).

My study was restricted by the weather, because tropical storms and hurricanes rendered some string data (e.g. maps of individual movement and distance moved) unusable. However, the use of thread bobbins was an efficient means of determining distances travelled, developing fine-scale maps of animal movement, and identifying microhabitat (forest edge, core, open) selectivity. The study was also limited to the two

study sites, with only one fragmented and one non-fragmented environment. However, our results remain clear; distance moved by the copperheads predictably decreased from summer to fall in individuals at the non-fragmented site, whereas, distance moved surprisingly increased in individuals at the fragmented site during the same time period.

My results suggest that habitat fragmentation affects seasonal movement patterns. Living in a fragmented environment, such as the campus of Coastal Carolina University, encompassed by suburban or industrial sprawl that varies seasonally may cause disruptions to the endogenous behavior that animals exhibit. College campuses vary in population numerous times throughout the year as semesters commence and end. Fragmented environments surrounding vacation spots such as urban sprawl or national parks, may oscillate in population throughout the seasons as well. With the disruption of fluctuating activity levels comes the potential for a disruption in seasonal behavior in animals. Though the results of this study show an effect of multiannual disturbance levels on animal behavior in a fragmented landscape, more physiological and ecological research in more fragmented environments with fluctuating activity levels will need to be conducted in order to further identify the parameters at play.

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Table 1. Frequency of adult male, female, and juvenile *Agkistrodon contortrix contortrix* captured in a non-fragmented habitat, Waccamaw National Wildlife Refuge (WNWR) and a fragmented habitat, Coastal Carolina University (CCU), Horry, County, SC from May through October, 2016.

Location and Sex	Frequency
CCU	49
Female	21
Juvenile	27
Male	1
WNWR	25
Female	12
Juvenile	5
Male	8
Total	74

Table 2. Effective distance moved (EDM) tested as a function of varying combinations of macrohabitat (CCU or WNWR), season, and snake by using the Likelihood Ratio Test (LRT). Snake was incorporated as a random effect because numerous observations came from the individuals. Alone, macrohabitat and season were not significant factors; however, the interaction of macrohabitat and season was significant. More detailed information on how each variable individually affected EDM can be seen in Table 3.

Model	LRT test statistic	LRT p-value	R²
EDM ~ Snake	NA	NA	NA
EDM ~ Macrohabitat + Snake	2.5899	0.1075	0.026
EDM ~ Season + Snake	3.0939	0.2129	0.027
EDM ~ Macrohabitat + Season + Macrohabitat*Season + Snake	4.8081	0.02833 *	0.065

Table 3. The individual effects on the effective distance moved (EDM) for the southern copperhead in a fragmented (CCU) and non-fragmented (WNWR) environment. Not all interaction coefficients were possible (i.e., the coefficient for Spring) to estimate due to sparse data.

Linear mixed effect models for distance moved					
Effective Distance Moved	Fixed effects	Estimate	95% CI	<i>t</i> value	<i>P</i>
	Intercept	56.51	41.10, 71.31	6.88	<<0.001
	Macrohabitat				
	WNWR	-26.90	-49.02, -4.70	-2.21	0.0369
	Season				
	Spring	-0.54	-20.44, 19.63	-0.05	0.9612
	Summer	-20.50	-40.24, -0.65	-1.88	0.0745
	WNWR*Summer	31.68	3.96, 60.53	2.06	0.0513
	Random effects	Variance	±SD	% var	
	Snake ID (<i>n</i> = 42)	103.8	10.19	9.15	
	Error	1031.2	32.11	90.85	

Table 4. Straight-line distance (SLD) was tested as a function of varying combinations of macrohabitat (CCU or WNWR), season, and snake by using the Likelihood Ratio Test. Snake was incorporated as a random effect as numerous observations came from the individuals. Neither the fixed effects nor the interaction effects had a significant contribution in predicting SLD.

Model	LRT test statistic	LRT p-value	R²
SLD ~ Snake	NA	NA	NA
SLD ~ Macrohabitat + Snake	0.2045	0.6511	0.001
SLD ~ Season + Snake	0.2601	0.8781	0.002
SLD ~ Macrohabitat + Season + Macrohabitat*Season + Snake	0.4545	0.5002	0.005

Table 5. The individual effects on the straight-line distance moved (SLD) for the southern copperhead in a fragmented (CCU) and non-fragmented (WNWR) environment. Not all interaction coefficients were possible (i.e. the coefficient for Spring) to estimate due to sparse data. None of the variables examined provided significant influence on the response.

Linear mixed effect models for distance moved					
Straight- line Distance Moved	Fixed effects	Estimate	95% CI	<i>t value</i>	<i>P</i>
	Intercept	26.30	13.91, 38.76	4.02	<<0.001
	Macrohabitat				
	WNWR	-7.98	-27.49, 11.33	-0.78	0.4385
	Season				
	Spring	5.47	-12.26, 23.53	0.58	0.5631
	Summer	0.15	-16.35, 16.09	0.02	0.9858
	WNWR*Summer	7.06	-16.48, 31.35	0.57	0.5716
	Random effects	Variance	±SD	% var	
	Snake ID (<i>n</i> = 42)	32.16	5.67	3.14	
	Error	991.11	31.48	96.88	

Table 6. Results of three logistic models determining habitat location preference within macrohabitat. Percent probability is in regards to the habitat location listed over the reference location. At CCU, the core habitat is preferred 9.99% of the time against the edge habitat, whereas at WNWR, the core is preferred 54.21% of the time against the edge. Both edge and core habitats were preferred over open habitats at CCU and WNWR.

Macrohabitat	Habitat Location	Reference	Probability (%)
CCU	Core	Edge	9.99
WNWR			54.21
CCU	Edge	Open	99.60
WNWR			89.41
CCU	Open	Core	0.18
WNWR			2.57

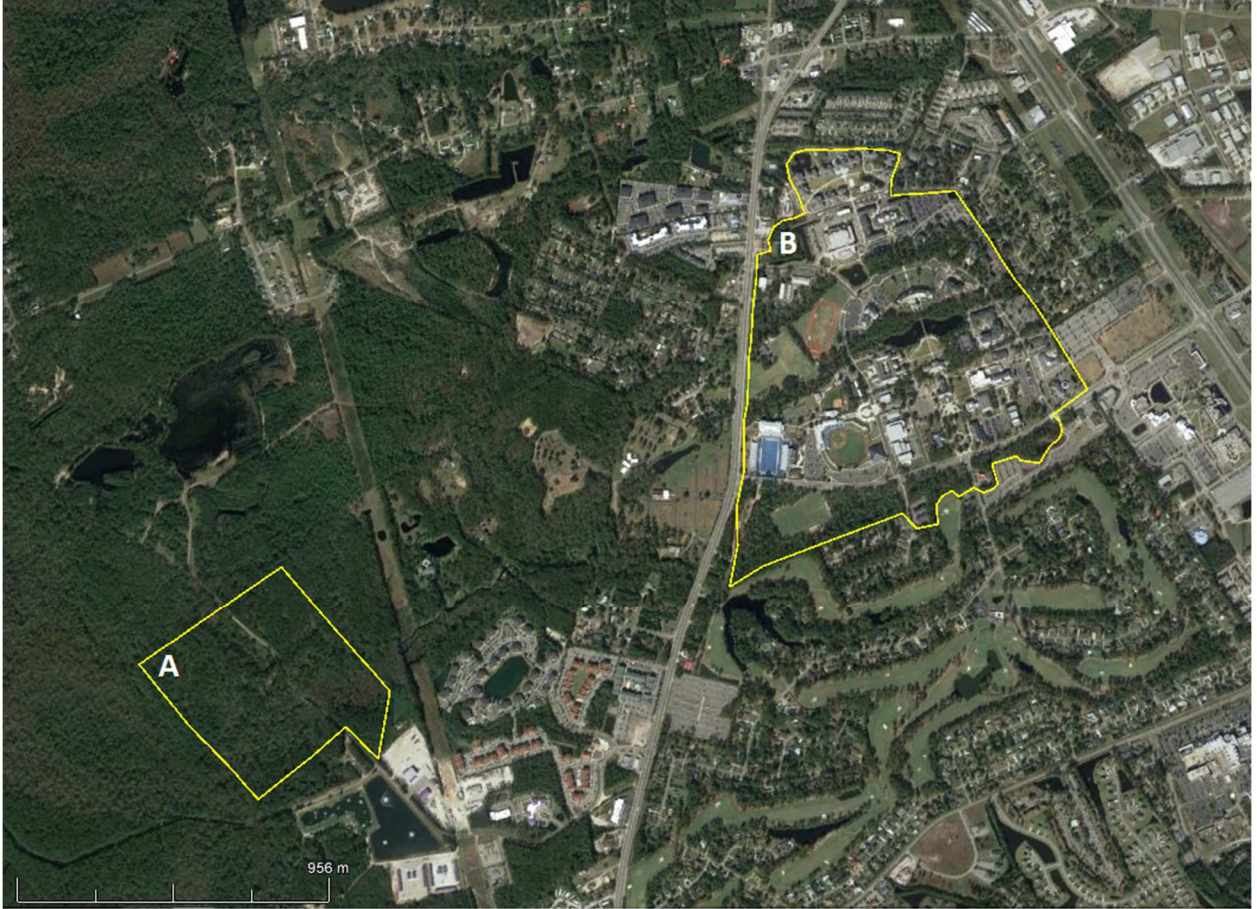


Figure 1. Non-fragmented, Waccamaw National Wildlife Refuge (A) and Fragmented, Coastal Carolina University (B) field sites located in Conway, Horry County, SC.

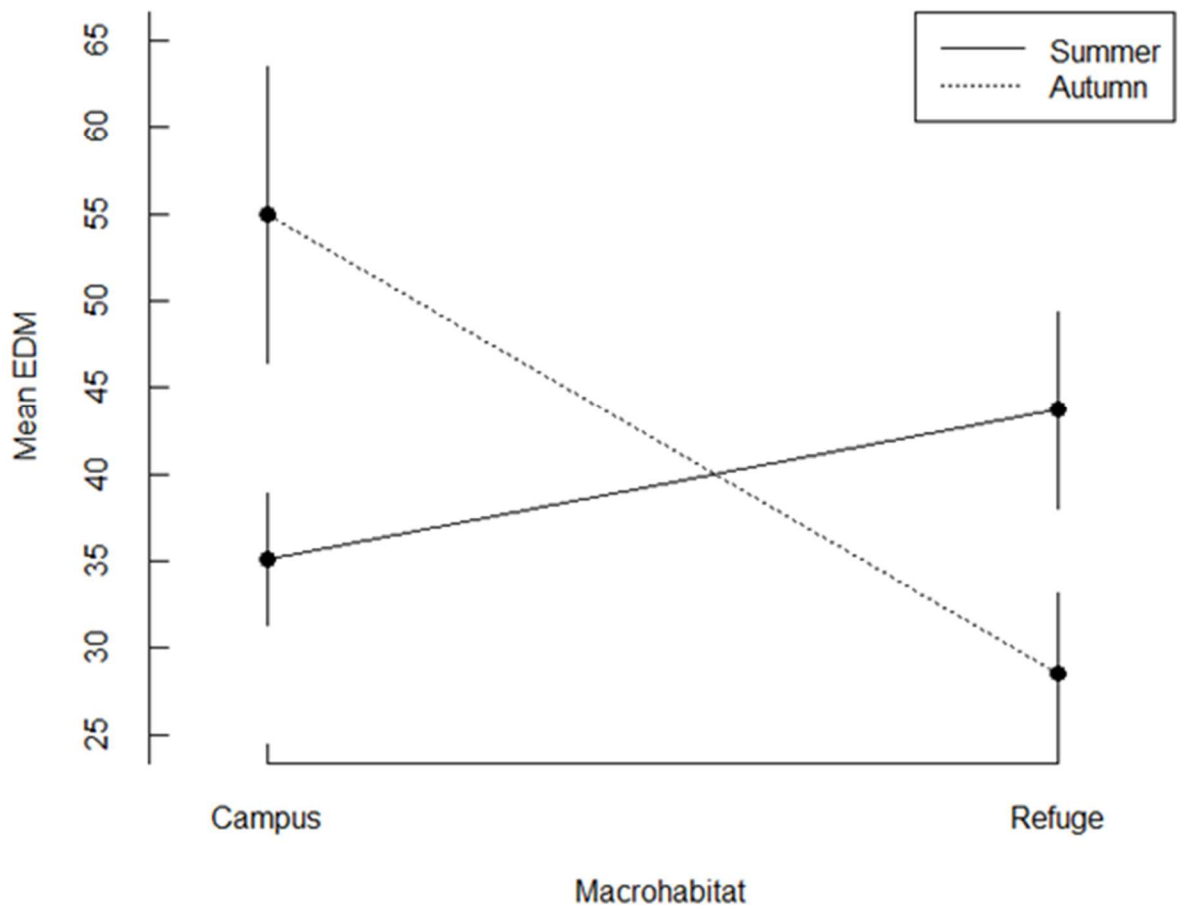


Figure 2. Effective distance moved (EDM, m) as a function of macrohabitat (non-fragmented vs fragmented) and season (summer, autumn). Spring is not included in this interaction as there were no observations from copperheads at CCU during the spring. Error bars are ± 1 SE.

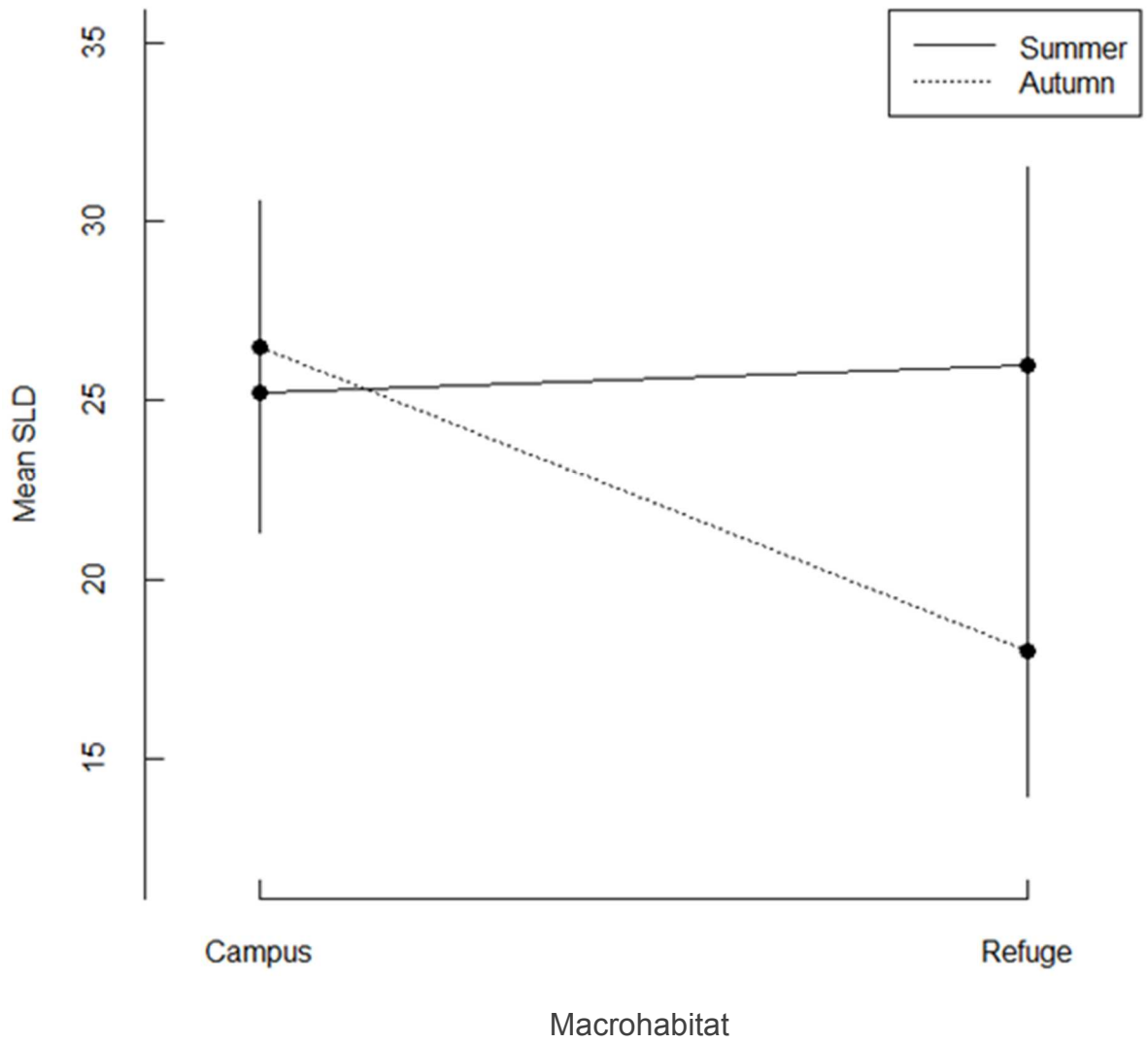


Figure 3. Straight-line distance (SLD) as a function of macrohabitat (non-fragmented versus fragmented) and season (Summer, Autumn). Error bars are ± 1 SE.

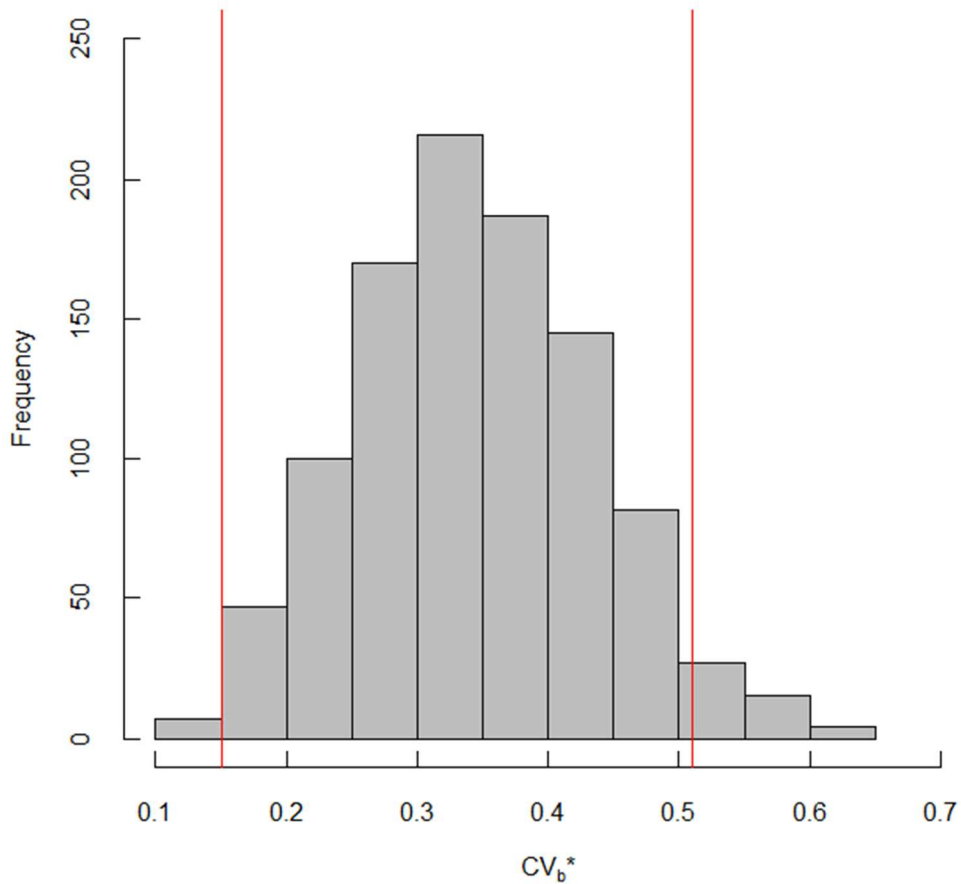


Figure 4. Histogram of the frequency of one thousand Cramer's V samples bootstrapped to address the issue of dependence among repeated samples. One habitat location (forest core, edge, open) was randomly selected from each of the snakes' observations one thousand times. A Cramer's V of 0 indicates the variables are independent, a Cramer's V of 0.2 indicates a moderate relationship between the variables, and a Cramer's V of 0.5 indicates a very strong relationship (close to redundant) between the variables. The Cramer's V calculated from this dataset was 0.35, indicating a strong relationship between habitat location (forest edge, core, or open) and macrohabitat (fragmented or non-fragmented study site). Vertical lines indicate the confidence interval boundaries.

CHAPTER II: MICROHABITAT USE BY THE SOUTHERN COPPERHEAD (*AGKISTRODON
CONTORTRIX CONTORTRIX*) IN A FRAGMENTED AND NON-FRAGMENTED HABITAT

INTRODUCTION

Habitat fragmentation is an important contributing factor to loss of biodiversity (Pereira et al. 2010, Rands et al. 2010). Studying both threatened and non-threatened taxa in fragmented environments can help better determine the structural requirements of species existing in affected habitats. The loss of continuous habitat and associated increase in solar radiation and decrease in moisture may change the structure, species composition, and functionality of the fragmented patches (Lindenmayer and Fischer 2006). Habitat fragmentation negatively affects biodiversity, but it is unclear which consequences of fragmentation (e.g. changes to temperature and moisture, dispersal limitations, microhabitat alterations) are most detrimental to long-term species survival (Didham et al. 2012, Fahrig 2013, Haddad et al. 2015). The consequences of habitat fragmentation are frequently viewed on a landscape scale, where fragmentation may affect gene flow among populations by reducing or preventing immigration and emigration (Petren et al. 2005). Habitat fragmentation, however, may also influence animal behavior by altering microhabitat characteristics within habitat patches (Laurance et al. 2002, Harrison et al. 2015). For example, separation of contiguous areas of habitat into isolated habitat patches results in increased relative area of edge environments. Edges of habitat patches form sharp ecotones that separate the interior of the habitat patch from the altered surrounding landscape.

Density, height, composition of ground cover, and canopy cover are important variables that determine structure, complexity, and overall quality of microhabitats (Ranius et al. 2008, MacGregor-Fors and Schondube 2011, Yang et al. 2015). For example, structural complexity of plant communities may influence availability of food, shelter, brumation or hibernation sites, predation risk, and competitive interactions (Brawn et al. 2001, Morris 2003, Mayor et al. 2009). Microhabitat selection is an

important process by which organisms choose a location relative to available alternative locations based on the organism's physiological/nutritional requirements (Heath 1970, Bauwens et al. 1996, Munguia et al. 2017). Determining the relationship between microhabitat composition and habitat selection helps to explain species-specific microhabitat requirements and potential consequences of habitat fragmentation on behavior and habitat use. Accordingly, habitat fragmentation may alter the range of microhabitats available to a given species. If so, fragmentation is predicted to result in differences in microhabitat use in fragmented versus non-fragmented environments (Murcia 1995, Laurance et al. 2002).

The southern copperhead is considered an ecological generalist, and occurs in a variety of habitats including pine savannahs, hardwood forests and bottomlands, agricultural farmlands, as well as suburban environments in the southeastern U.S. (Bachleda 2001, Conant et al. 2016). Habitat generalist are capable of surviving in a wide range of environmental conditions and therefore are predicted to be relatively insensitive to habitat fragmentation. My objective was to determine if microhabitats for the southern copperhead in a fragmented, suburban habitat differs from suitability in a relatively undisturbed, non-fragmented habitat. To accomplish this objective, we quantified microhabitat use of copperheads at two sites in Horry County, South Carolina, USA.

METHODS

Study sites

Copperheads were captured from May 2016 through October 2016 (n=74 snakes) at two sites differing in amount of habitat fragmentation in Horry County, South Carolina (Figure 1). The fragmented site (n = 49 snakes), was located on the campus of

Coastal Carolina University (CCU; 33.795°, -79.012°). Habitat in the fragmented site consisted of relatively small patches of forest (approximate patch size 1.66 ha) resulting from secondary succession. These patches were separated by buildings, parking lots, athletic fields, and paved roads. The non-fragmented site (n = 25 snakes), was located within the Waccamaw National Wildlife Refuge (approximately 27.74 ha, 33.785°, -79.039°). Habitat at this site consisted of continuous southeastern pine and hardwood forest and swamp bottomland bisected by foot trails and a single dirt road.

Tracking procedures

Southern copperheads were located by active searching from 0700 h to 2200 h in both study sites throughout the forest core, edge, and open. Copperheads were almost exclusively located in forest core and edge habitats. The snakes were captured using Gentle Giant™ snake tongs (Midwest Tongs, Greenwood, MO). After capture, snakes were placed into a 5-gallon plastic bucket until processed for attachment of thread bobbins. We quantified microhabitat use by the southern copperhead by attaching thread bobbins (0.00625 lb, < 1% of the average mature snake body weight, Imperial Threads Inc., Northbrook, IL) to adult snakes and recording the locations of individuals throughout their daily activity period. Thread bobbins were attached externally to the posterior $\frac{3}{4}$ length of the snake using 3M Transpore™ medical tape (3M, St. Paul, MN, 1 in x 10 yd). The loose end of the thread bobbin was tied to a stake in the ground or a tree trunk to allow the string to pull freely from the bobbin as the snake moved. The snake was thereafter tracked every 48 hours by following the string from the location where the individual was last seen (i.e. where the loose end of the string was tied). Tracking times alternated between morning (0700 – 1100 h), afternoon (1200 – 1600 h), and evening (1800 – 2100 h). When a snake was located at each time period, microhabitat choices were recorded.

Microhabitat analysis

When a copperhead was located, we captured it using “Gentle Giant” snake tongs (Midwest Tongs, Greenwood, MO) and placed it in a 5-gallon plastic bucket while microhabitat variables were recorded. The longitude and latitude of each individual was recorded using a handheld GPS device with an accuracy of ± 3 m (GPSmap 62s, Garmin International Inc., Olathe, KS). A 1 m² quadrat was placed around the capture location of each snake for quantification of microhabitat characteristics. In this study, snake microhabitat was defined as the 1 m² area around the snake’s capture location. We assessed 1m² to be an appropriate estimate of the microhabitat occupied by southern copperheads because mature copperheads are approximately 60 cm long, and when coiled and stationary, they occupy a relatively small surface area of their microhabitat. In the understory habitat where copperheads occur, a change in distance of as little as one meter may expose the snake to a microhabitat with a vastly different physical environment compared to the snake’s selected location.

An area of 5 m² was delineated around each snake’s capture location with the point of capture being the center point of the 5 m² quadrat. The 5 m² quadrat was further divided into 25 individual 1 m² quadrats. Each of these individual quadrats were labelled 1 through 25, with 13 being the point of capture (Figure 2). A random number, 1 through 25 (13 excluded), was selected and the 1 m² quadrat associated with the random number was used for the background microhabitat analysis. Background sites within 2.5 m of the capture location represent available microhabitats that were not chosen by individual snakes in lieu of absence data.

Microhabitat variables consisted of number of trees, number of woody plant stems, number of herbaceous vegetation stems, percent grass cover, and percent canopy cover within each 1 m² quadrat. Trees were defined as woody vegetation with

trunk ≥ 152 mm in diameter, woody vegetation was defined as vegetation with wood stems < 152 mm, and herbaceous vegetation was defined as non-woody, annual vegetation. Percent grass cover was defined as the overall percentage of grass that covered the two-dimensional space occupied within the quadrat and was independently confirmed by two people. Percent canopy cover was measured using a spherical crown densiometer (Forestry Suppliers Inc., Jackson, MS).

Data analysis

A habitat suitability model was fitted using R statistical software (R version 3.3.2; R Core Team 2016). To identify the most important features associated with snake microhabitat, a single logistic regression model was used and contained the following variables: number of trees, number of woody vegetation stems, number of herbaceous vegetation stems, percent grass coverage, percent canopy cover, macrohabitat (fragmented or non-fragmented), the interaction of macrohabitat with all of the variables listed, and the random effect of snake ID. Variance inflation factors were calculated for the mixed effect model. The variance inflation factors were < 2 for all variables and therefore none were removed from the regression model (Zuur et al. 2010). The model was selected using Bayesian Information Criterion (BIC; Schwarz 1978); the fixed effects were back-fitted, the random effect was forward-fitted, and the fixed effects were re-back-fitted using Package 'LMERConvenienceFunctions'. Fixed effects were back-fitted twice because the inclusion of random effects can potentially render some fixed effects non-significant (Tremblay and Tucker 2011, Newman et al. 2012). Information loss (Δ BIC; Raftery 1995) is the difference between the BIC value for Model i and the model with the smallest BIC value. Information loss increases as evidence against a model increases, relative to the model with the minimum BIC value (Raftery 1995, Link and Barker 2006). Schwarz weight (ω) is the probability that Model i is the true model,

assuming that the true model resides in the all-inclusive regression model provided (Link and Barker 2006). Once a model was chosen, differences in accuracy, sensitivity, specificity, and AUC (area under the receiver operating characteristic curve) were reported for that model.

RESULTS

Snakes were tracked individually to obtain a total of 291 observations. Of these 291 observations, 276 were used for collecting microhabitat data associated with snake location. Microhabitat data were collected for 255 random background locations where snakes were not observed. Overall, the number of trees, woody vegetation stems, herbaceous vegetation stems, percent grass cover and percent canopy cover were similar between the fragmented and non-fragmented sites, but differences were notable between the snake-presence microhabitats and the background microhabitats (Table 1). Percent canopy cover was higher in the snake-presence microhabitats (approximately 12.5% higher). Number of herbaceous vegetation stems were also higher in the snake-presence microhabitats, though percent grass cover was higher in the background microhabitats.

Of the variables put into the logistic regression model, the best fit model contained herbaceous vegetation and percent canopy cover ($\omega_1 = 0.47$; Table 2). The accuracy of this model was approximately 73%. The sensitivity and specificity of the model had proportions of 0.65 and 0.81, respectively. The area under the receiver operating characteristic curve (Figure 3) was 0.76. There was no difference in the two variables selected by the best fit model (i.e. number of herbaceous stems and percent canopy cover) between the fragmented and non-fragmented sites (each interaction $\omega_i < 0.001$).

DISCUSSION

As a habitat generalist, the southern copperhead inhabits contiguous woodlands as well as suburban environments (Bachleda 2001). Habitat generalists are able to thrive in a variety of habitats differing in spatial scale (Root 1967, Forman 1997, and Golden and Crist 1999). For example, in the present study, the microhabitats most suitable for copperheads were available at both the smaller fragmented and larger non-fragmented sites. However, the model selected indicates that copperheads preferred specific microhabitats found within both study sites (i.e. presence of herbaceous vegetation and high canopy cover). If the copperheads were behaving as a habitat generalist, using a range of microhabitats, the AUC value of our selected model would be closer to 0.50. In contrast, the AUC was 0.76 indicating the snakes were behaving as a habitat specialist, using a specific subset of microhabitat features within both study sites. The southern copperhead was able to find the same preferred microhabitat features in the fragmented site as they were in the non-fragmented site. Our results indicate that although copperheads have relatively clear microhabitat preferences, these microhabitats are fairly common in South Carolina and therefore permit the species to exist in a broad range of macrohabitats. The effects of fragmentation are more detrimental if a species' microhabitat requirements are highly localized and not widely distributed. For example, suitable microhabitats for the broad-headed snake (*Hoplocephalus bungaroides*) are limited in south-eastern Australia, restricting individuals to re-using refugia instead of expanding out (Croak et al. 2013).

The number of herbaceous stems and percent canopy cover were the two variables best explaining habitat suitability of *A. contortrix*. An area value of 0.76 under the ROC curve indicates that the selected model was able to discriminate between

locations where snakes were observed versus background locations representing microhabitat available to snakes but not used. Presence of snakes at both study sites was associated with higher herbaceous cover as well as percent canopy cover, compared to the background locations. Both herbaceous vegetation and canopy cover may provide protective cover from predators and influence the behavior of both predator and prey species. For example, mammals and birds are more alert when foraging away from tree and shrub cover (Barnard 1980, Leger et al. 1983, Cassini 1991, Otter 1994, Tchabovsky et al. 2001, Ebensperger and Hurtado 2005). Similarly, small rodents forage less often in open areas away from vegetative cover (Newman et al. 1988, Brown and Alkon 1990, Brown et al. 1992, Hughes and Ward 1993, Orrock et al. 2004). In addition, rodents may experience increased predation when active in open habitat without canopy cover (Longland and Price 1991). *Agkistrodon contortrix* is likely preyed upon by birds as well as mammals and other snakes (Steen et al. 2014). Both tree canopy cover and herbaceous vegetation could provide protection from avian predators and herbaceous vegetation could provide cover to help snakes avoid detection by terrestrial predators.

The ecology of ectotherms is highly dependent on the thermal features of their habitats (Huey 1982, Huey and Kingsolver 1989, Pringle et al. 2003). Most ectotherms use microhabitats to regulate their internal temperatures (Bogert 1949, Bartholomew 1964, Kearney et al. 2009). In wooded environments, ground temperature is directly affected by radiation input through gaps in the canopy (Pringle et al. 2003). Most snake observations occurred in the forest core and edge with a notable lack of observations in the open environment; it is likely that the copperheads were using herbaceous vegetation and canopy cover for thermoregulation as well as predator avoidance. Vegetative cover provides shaded and therefore cooler microhabitats that aid in thermoregulation during hot summer months in South Carolina (Parker 2014).

Our results indicate that habitat fragmentation may not be detrimental to a given species if the required microhabitat conditions are available in both fragmented and non-fragmented environments and the size of the habitat does not restrict movement. Fragmentation partitions macrohabitats (Fahrig 2003), but may not always alter microhabitat features. For example, Hristovski et al. (2016) found that the most mobile ground beetles (e.g. *Myas chalybaeus* and *Tapinopterus balcanicus*) were not vulnerable to fragmentation and persisted in high numbers in the microhabitats of each of their three study sites. If the area encompassed by the home range of an animal is viewed as a suite of microhabitats, the effect of habitat fragmentation may be dependent on which of their microhabitats have been altered, as well as their availability. In addition, animals with small home ranges could persist in appropriate microhabitats within relatively small patches. For example, lungless salamanders (*Plethodontidae*) have comparatively small home ranges due to their moisture and humidity requirements, and correspondingly some species are able to persist in relatively small, isolated populations (Spotila 1972, Feder 1983, O'Donnell et al. 2014). In contrast, tiger salamanders (*Ambystoma tigrinum*) have larger home ranges resulting from individuals leaving permanent ponds and moving considerable distances to profitable breeding ponds annually (Denoel et al. 2007). Tiger salamanders and other species with larger home ranges may be more negatively affected by habitat fragmentation. These observations do not negate the negative effect of fragmentation on dispersal (Hanski 1999, Prugh et al. 2008) and gene flow (Manel et al. 2003, Segelbacher et al 2010).

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Table 1. A summary of the microhabitats (mean \pm SE), organized by microhabitat type (snake presence or background) and macrohabitat.

	Snake Presence Microhabitats (mean \pm SE)	Background Microhabitats (mean \pm SE)
Both Sites		
Num. Trees	0.56 \pm 0.08	0.43 \pm 0.06
Num. Woody Vegetation	9.93 \pm 1.07	9.77 \pm 1.05
Num. Herbaceous Vegetation	9.70 \pm 1.06	6.84 \pm 0.77
Percent Grass Cover	7.55 \pm 1.29	9.80 \pm 1.52
Percent Canopy Cover	90.91 \pm 0.81	78.33 \pm 1.33
Fragmented Site		
Num. Trees	0.94 \pm 0.17	0.60 \pm 0.11
Num. Woody Vegetation	7.56 \pm 1.00	9.26 \pm 1.72
Num. Herbaceous Vegetation	7.26 \pm 1.42	6.25 \pm 1.36
Percent Grass Cover	3.38 \pm 1.10	10.13 \pm 2.48
Percent Canopy Cover	91.10 \pm 1.40	79.58 \pm 2.24
Non-fragmented Site		
Num. Trees	0.25 \pm 0.05	0.28 \pm 0.06
Num. Woody Vegetation	11.88 \pm 1.75	10.19 \pm 1.29
Num. Herbaceous Vegetation	11.71 \pm 0.53	7.32 \pm 0.85
Percent Grass Cover	10.97 \pm 2.12	9.53 \pm 1.89
Percent Canopy Cover	90.78 \pm 0.97	77.30 \pm 1.56

Table 2. List of competing fixed effects that were tested as individual logistic regression models to determine which factors best define suitable habitats for the southern copperhead (*Agkistrodon contortrix contortrix*). Bayesian information criterion (BIC) values were used to rank the candidate models. Δ BIC represents the difference in BIC values between Model *i* and the model with the minimum BIC value. Schwarz weights (ω) were calculated and are defined as the probability that Model *i* is the true model, assuming that the true model is included in the models examined. The lowest BIC value and the highest Schwarz weight correspond with the most likely model. Every model also includes the random effect of snake ID. “Macro” = macrohabitat (fragmented and non-fragmented); “veg” = vegetation.

Model	n parameters	BIC	ΔBIC	ω_i
Macro x Herbaceous Veg	3	504	36	< 0.001
Macro x Woody Veg	3	499	31	< 0.001
Macro x Grass Percent	3	494	26	< 0.001
Macro x Tree	3	489	21	< 0.001
Macro x Canopy Cover	3	489	21	< 0.001
Woody Veg	2	489	21	< 0.001
Macro	2	483	15	< 0.001
Grass Percent	2	477	9	0.005
Tree	2	472	4	0.063
Herbaceous Veg	2	468	0	0.466
Canopy Cover	2	468	0	0.466

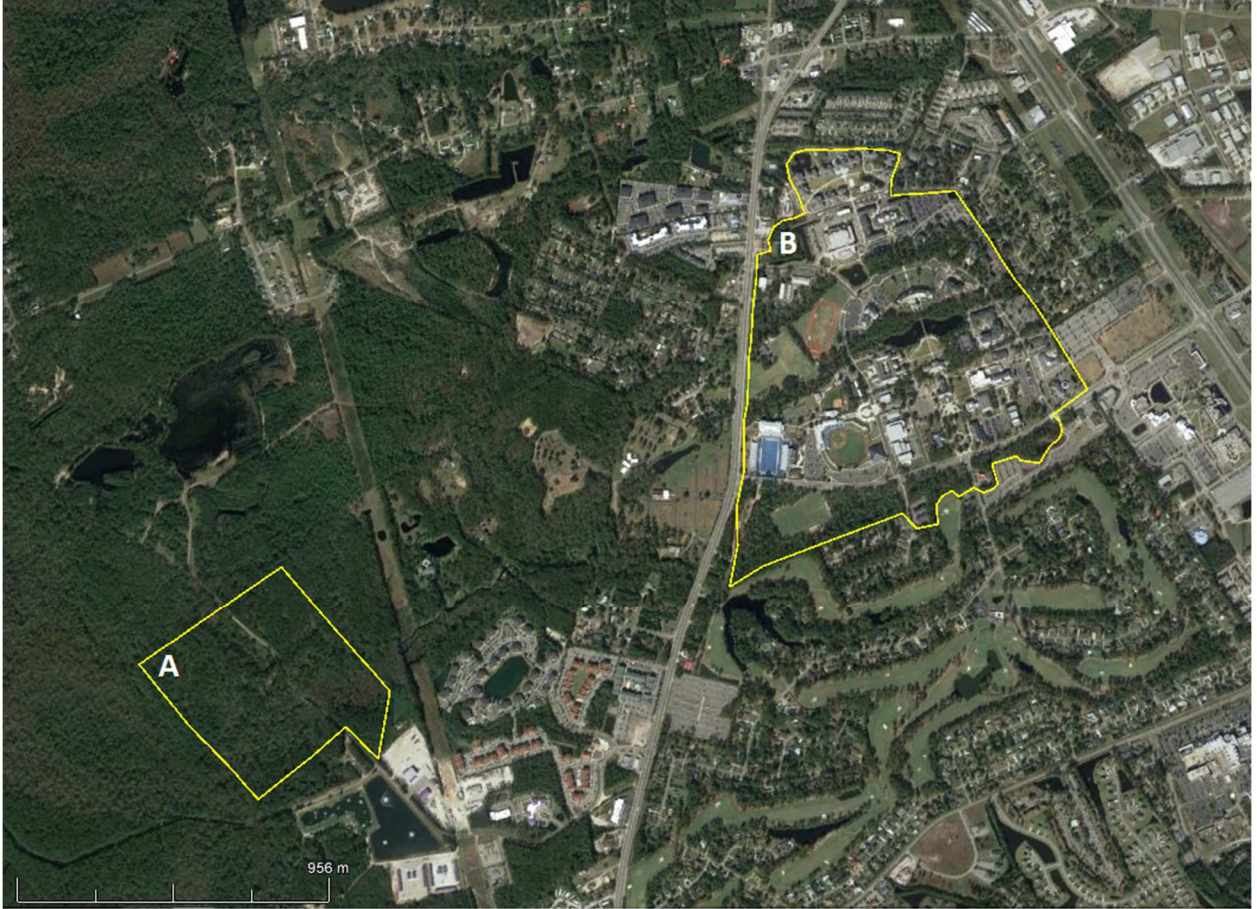


Figure 1. Non-fragmented, Waccamaw National Wildlife Refuge (A) and Fragmented, Coastal Carolina University (B) field sites located in Conway, Horry County, SC.

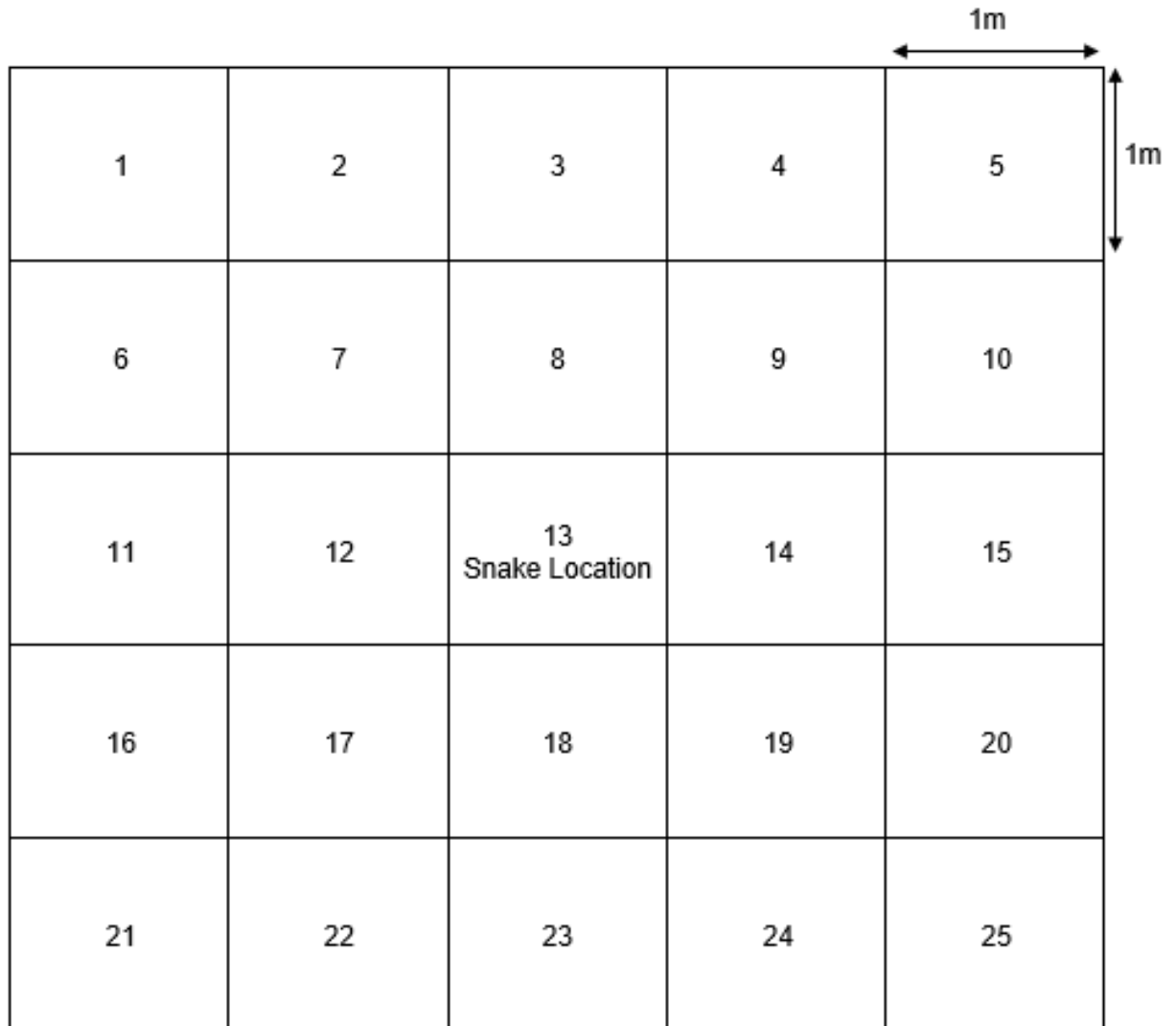


Figure 2. An illustrated example of the numbered 5m x 5m plot surrounding the location where the snake was located or re-located. Each numbered square represents a 1m x 1m quadrat, of which one was picked through use of a random number generator, excluding 13 as that was plot the snake was located in. Microhabitat composition data was collected in plot 13 and noted as the microhabitat selected by the snake. Composition data for the background microhabitat, pseudo-absence location, was collected at the plot that corresponded with the randomly generated number.

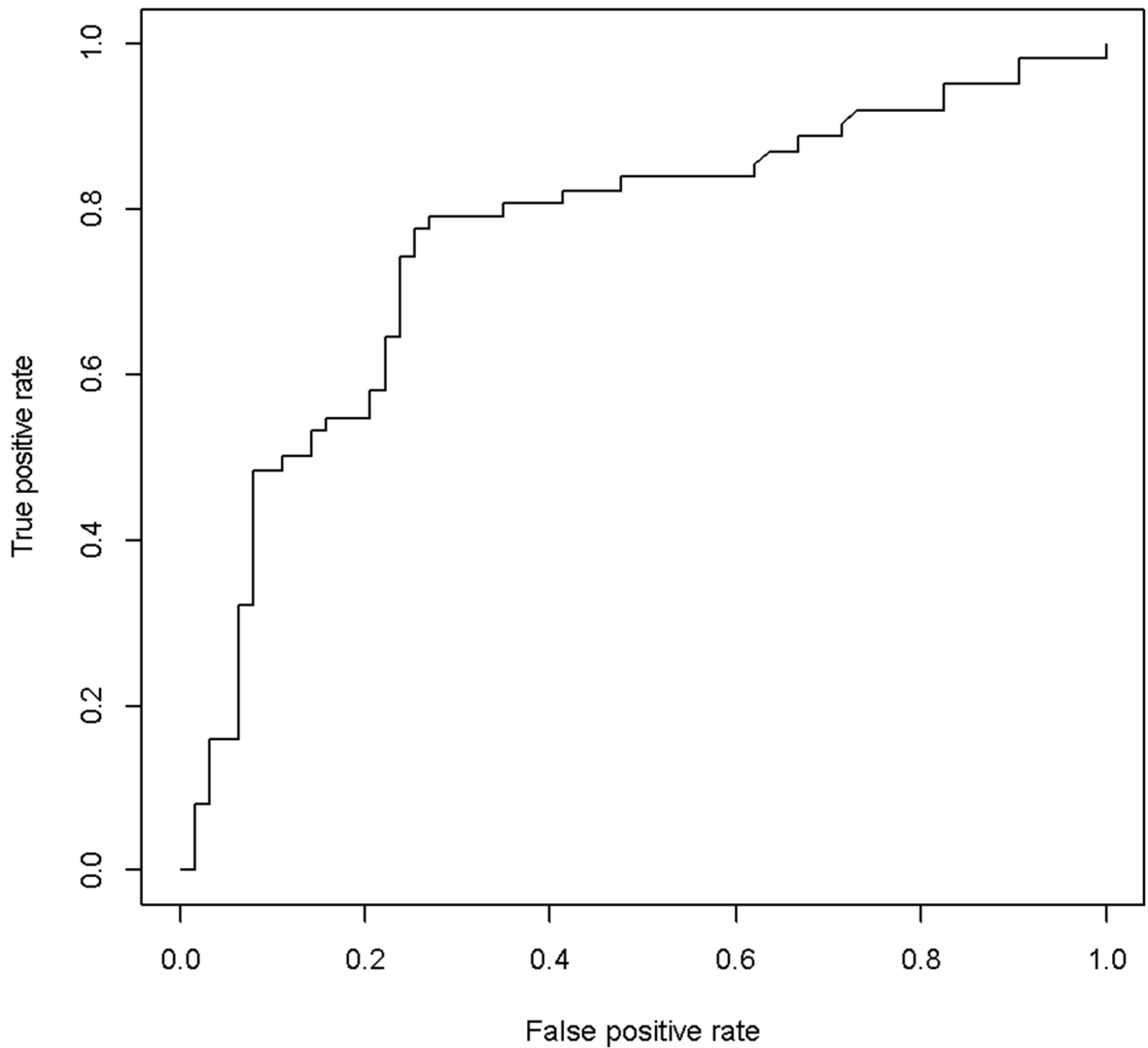


Figure 3. The receiver operating characteristic curve of the best fitted model for microhabitat suitability of the southern copperhead (*Agkistrodon contortrix contortrix*). The area under the curve was calculated at 0.76, discerning a definite discrimination between snake presence locations and background, or pseudo-absence locations.

