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Spatial ecology and multi-scale habitat selection of the Copperhead (*Agkistrodon contortrix*) in a managed forest landscape

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ABSTRACT

We evaluated the spatial ecology and habitat use of the Copperhead (*Agkistrodon contortrix*) in managed, pine-hardwood forests in the William B. Bankhead National Forest, Alabama. We used radiotelemetry to monitor 31 snakes (23 males, 8 females [5 gravid and 3 non-gravid females]) over a period of 3 years (2006–2008). Snakes were tracked for one or more seasons in a series of 18 forest stands composed of 6 treatments (Control, Burn, Light Thin, Heavy Thin, Light Thin with Burn, and Heavy Thin with Burn) replicated three times. Home-range estimates for male snakes averaged 17.8 ± 2.3 (based on Utilization Distributions [UD]) and 12.0 ± 1.9 ha (based on 100% Minimum Convex Polygons [MCP]), whereas home-range estimates for gravid female snakes averaged 7.1 ± 1.8 ha (based on UD) and 4.1 ± 1.1 ha (based on MCP) and were significantly different between both sexes for all home-range analyses. We did not detect an effect of forest management on home-range size of male snakes. Macrohabitat use differed among male and gravid female snakes, where male snakes used edge (field and secondary road edges) and Southern Pine Beetle macrohabitats in significantly greater proportion than what was available. Gravid female snakes did not use macrohabitats differently than what was available, but tended to use thinned stands and forest stand canopy gaps for parturition sites. Microhabitat use patterns were similar between male and gravid female snakes, where both sexes tended to use microhabitat sites with relatively greater litter depth and coarse woody debris percent cover compared to random microhabitat sites. Microhabitat use patterns for male snakes tended to differ based on forest management treatment (Thin and Thin with Burn versus Control and Burn stands), where selected microhabitat sites had lower ambient and soil temperatures compared to random sites in thinned stands. Collectively, we illustrated that male *A. contortrix* displayed hierarchical habitat use, whereas female *A. contortrix* displayed preference for habitat features at the microhabitat scale only. Overall, our short-term study provides evidence that recently-thinned pine-hardwood stands are not initially used at a frequency greater than their availability, which suggests that microhabitat and microclimate conditions likely limit use immediately following management.

1. Introduction

Increasing evidence of worldwide biodiversity declines illustrates the heightened need to understand biological requirements of both common and rare species (Cincotta et al., 2000; Myers, 1996; Sodhi et al., 2004). This is particularly true for smaller vertebrates, such as reptiles that have not received the level of public attention as other charismatic megafauna. As with other taxa, habitat destruction through anthropogenic means and alteration of natural disturbance regimes have been suggested as one of the major factors behind declines of reptile populations (Böhm et al., 2013; Garber and Burger, 1995; Germaine and Wakeling, 2001). Forest management in the form of timber harvest and prescribed burning provides a valuable tool to manage and/or restore degraded forest ecosystems (Dellasala et al., 2003). As these disturbances generally impact large areas, the concomitant changes in microclimate and microhabitat conditions can impact biological and physiological requirements of reptiles (Gram et al., 2001; Provencher et al., 2003; Sutton et al., 2014). Herpetofaunal

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responses to forest management are relatively well-documented (e.g., Russell et al., 2004); however, most studies have either focused solely on amphibian responses (e.g., deMaynadier and Hunter, 1995; Semlitsch et al., 2009; Tilghman et al., 2012), or have reported on a limited portion of the reptile fauna (e.g., Greenberg and Waldrop, 2008; Greenberg et al., 1994; Lunney et al., 1991; Vitt et al., 1998).

Limited published work exists regarding snake responses to forest management; however, recent studies revealed that litter-dwelling snakes responded negatively to clearcut management (Todd and Andrews, 2007), and species of medium-large snakes (e.g., Black Racers [*Coluber constrictor*]) were more abundant after forest thinning in pine-hardwood stands (Sutton et al., 2013). Large-bodied snakes have proven difficult to sample given issues with inadequate sampling methods (e.g., Enge, 2001) and difficulties with detection of cryptic and secretive species during visual and passive surveys (Ryan et al., 2002; Steen, 2010). Most studies of herpetofaunal responses to forest management rely primarily on stationary drift-fences to sample reptile populations, and it is likely that these studies underestimate the responses of species with activity ranges larger than the primary study area. This is particularly true for species that primarily use managed landscapes as a corridor to access other preferred and selected habitats.

Organisms may exhibit varied habitat use patterns at different spatial scales (Compton et al., 2002; Harvey and Weatherhead, 2006; Orians and Wittenberger, 1991; Wiens et al., 1987). Habitat use in snakes is understood to proceed in a hierarchical fashion where selection is initially regulated by internal physiological factors (e.g., digestive state and reproductive condition; Reinert, 1993). Snakes then use suitable habitats at the landscape scale (e.g., deciduous forest, field edge, grassland) based hierarchically on suitable microhabitat features (e.g., litter depth, coarse woody debris cover) within these landscape units (Harvey and Weatherhead, 2006; Row and Blouin-Demers, 2006) that correspond with small-scale biological interactions (e.g., temperature preferences, prey odors, and intraspecific relationships; Reinert, 1993). The nature in which a focal organism exhibits habitat use may lead to important and different conservation and management decisions. For example, a species may display uneven preference for certain microhabitats and partition this use within distinct landscape units (hierarchical habitat use), whereas another species may display preference for certain microhabitats without preference for habitats at the landscape scale (Harvey and Weatherhead, 2006; Hoss et al., 2010; Moore and Gillingham, 2006; Waldron et al., 2008). Understanding the relationships between habitat use and spatial scale is important for species that require further conservation measures or habitat management (Mayor et al., 2009).

The spatial arrangement of biological resources (e.g., gestation and hibernation sites) is one of the primary factors that determine how species use different components of the landscape. Snakes, like most other vertebrates allocate activity patterns in accordance with biological needs. For example Bushar et al. (1998) examined relationships among yearly movements, hibernation site location, and genetic relationships of Timber Rattlesnakes (*Crotalus horridus*) and found snakes that used the same hibernacula yearly were more closely related to each other compared to snakes that used geographically-separated hibernation sites. The authors found that female snakes were more likely to use basking sites located closest to hibernacula and were more likely to breed with males from the same hibernation sites. Additionally, in studies of Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*), the spatial arrangement of hibernation and summer foraging sites correlated with movement length and home range size for this species; specifically, snakes in habitats with hibernation resources in close proximity to summer foraging habitats had considerably smaller home ranges compared to snakes occupying habitats with greater distance between these resources (Degregorio et al., 2011; Johnson, 2000; Marshall et al., 2006; Reinert and Kodrich, 1982). Habitat use studies that incorporate a spatial context have greater inference because habitat use and movement patterns are ultimately tied to the spatial arrangement of biological resources, which include sites for gestation, foraging, and thermoregulation (e.g., Moore and Gillingham, 2006; Richardson et al., 2006).

The alteration of environmental conditions via large-scale disturbances may influence snake spatial ecology and habitat use patterns. Although studies of snake habitat use and spatial ecology are abundant, detailed studies of how landscape disturbances impact habitat and space use are generally lacking (but see Cross et al., 2015; Durbian, 2006; Kjoss and Litvaitis, 2001; Reinert et al., 2011). The primary objective of this study was to use a mobile, poikilothermic vertebrate (Copperhead [*Agkistrodon contortrix*]) as a model species to evaluate the impacts of forest restoration treatments on habitat use and spatial ecology patterns at multiple spatial scales. We predicted that temperature and microhabitat variation within managed forest environments would impact both habitat use and spatial ecology patterns of *A. contortrix*. Specifically, we hypothesized that snakes in recently thinned forest stands would have greater home range size and different habitat use patterns compared to snakes inhabiting closed canopy stands. We predicted these differences would be due to the initial reduction in the availability of microhabitat cover features and subsequent alteration of movement patterns to locate such features in managed and adjacent unmanaged habitat patches.

2. Materials and methods

2.1. Study area

Our study was centered in the northern portion of the William B. Bankhead National Forest (BNF), which is located in Lawrence, Winston, and Franklin Counties in northwestern Alabama. The BNF is a 72,800 ha multi-use forest located along the highly dissected portion of the southern Cumberland Plateau (Gaines and Creed, 2003; Smalley, 1982). The BNF is composed largely of mixed pine-hardwood forests, except in areas where Loblolly Pine (*Pinus taeda*) was actively planted to re-establish forest conditions in abandoned agricultural and/or heavily-timbered areas (Gaines and Creed, 2003). During the late 1990s and early 2000s, Southern Pine Beetle (*Dendroctonus frontalis*) infestations resulted in large numbers of standing dead trees and increased fuel loads. To deal with increased fire risk and prevent further loss of standing timber crops, the BNF developed a long-term forest restoration plan (Gaines and Creed, 2003; Schweitzer and Tadesse, 2004) to restore *P. taeda*-dominated stands to historic oak-hickory stand conditions via prescribed burning and thinning. The forest stands evaluated during this study were generally located on upland sites and were composed primarily of *P. taeda* with most stands possessing a hardwood component (e.g., *Quercus* and *Carya* species). These stands were managed with a variety of forest treatments, including no treatment (control), prescribed burn (3–5 year return interval), light thin (17 m^2/ha residual basal area [BA]), heavy thin (11 m^2/ha residual BA), and two thin and burn interaction treatments (light thin with burn and heavy thin with burn). Each of these treatments (~9 ha in size) was replicated three times (18 total treatments) across the landscape within the northern portion of the BNF. We leveraged this pre-existing matrix of forest management practices to evaluate effects of forest management on snake spatial ecology and habitat use. For further information on forest stand conditions and forest management operations, please refer to Sutton et al. (2014, 2013, 2010).

2.2. Study organism

Agkistrodon contortrix is a widely-distributed pit-viper species with a geographic range that extends from southern Texas to Georgia and north into southern Connecticut, USA. This species (which is commonly encountered in the southeastern United States and is an important prey item for other snake species (Steen et al., 2014), was previously recognized as five sub-species; however, recent molecular analyses (Burbrink and Guiher, 2015) provided support for two distinct species, including the Eastern Copperhead (*Agkistrodon contortrix*) and the Broad-banded Copperhead (*Agkistrodon laticinctus*). We chose *A. contortrix* as a model organism for this study as they, (1) are common inhabitants of eastern and southeastern forests (Fitch, 1960), (2) are sit-and-wait predators and are likely to demonstrate clear habitat selection patterns, (3) have home-ranges that range from 6.1 to 44.5 ha (Smith et al., 2009), which coincide well with plot size and the surrounding habitat matrix of this study, and (4) habitat use and spatial relationships of *A. contortrix* are largely unknown and not reported for the southeast United States.

2.2.1. Snake capture and surgery procedures

We captured *A. contortrix* in modified drift-fence trap arrays used for a larger study that evaluated amphibian and reptile responses to forest management (Sutton et al., 2014, 2013, 2010) and during incidental surveys in designated research plots. We collected and radio-tagged snakes from different treatments as much as possible to acquire a representative sample across treatments. We determined snake sex via cloacal probes and determined female reproductive condition opportunistically, when possible, during surgery and by field observations (i.e., sedentary behavior (Reinert, 1984a) throughout the active season). Male snakes that were larger than 180 g and female snakes that were larger than 150 g were implanted intraperitoneally with a radiotransmitter (males: model SI-2 [9 g], females: model SB-2 [5 g]; Holohil Systems Ltd.) following the procedures in Reinert and Cundall (1982). We sterilized all surgery equipment in an autoclave prior to surgery and maintained sanitary conditions during surgery through the use of sterile latex gloves and disinfection of all surfaces with 90% ethanol. We anesthetized snakes with isoflurane and began surgical procedures when snakes were unresponsive to touch. Each snake was restrained in an acrylic snake tube to maintain anesthesia during surgery. We followed traditional transmitter implantation methods (i.e., Reinert and Cundall, 1982) except that we used a self-retaining retractor (Codman Surgical Instruments) to open the body cavity, which eased transmitter placement. We also used a 30.5 cm long aluminum tube (0.23 mm outside dia) to allow placement of the transmitter antenna between the skin and ribcage of the snake. We used a 3–0 dissolvable suture to close the inner body cavity and outer skin and used Nexaband (Abbott Laboratories) liquid topical tissue adhesive to further seal the suture site. On completion of surgical procedures, snakes were monitored in captivity for two days and then released near the original capture site.

2.3. Radiotelemetry procedures

After snakes were released, we relocated each individual every 5–7 days throughout the active season (April-November) using a Merlin 12 (Custom Electronics) or a TRX–48S (Wildlife Materials) receiver equipped with a three-prong yagi antenna. Tracking commenced primarily during daylight hours and as weather permitted. At each location, we recorded locality information ($\leq$6 m accuracy) using a handheld Garmin Etrex global positioning system. When a snake was located during a tracking event, we flagged the location along with a paired, random location (described in further detail below).

2.3.1. Home-range estimation

We determined home-range estimates for each snake that was tracked throughout a majority of the active season (April – November). To produce home-range estimates, we used the Animal Space Use v.1.3 (ASU) program, which permits evaluation of home-range patterns through an information-theoretic approach (Horne and Garton, 2006). This approach provides home-range estimates with significantly lower bias compared to a "one size fits all approach" by examining the overall movement patterns that best explain the space use of the individual. All area-usage techniques have assumptions and limitations (Marshall et al., 2006) and it is important to estimate home-range use patterns based on the fit of the data rather than choosing an approach based on personal preferences and trends in the literature (Horne and Garton, 2006). Furthermore, each home range model estimated by the ASU program (besides the Kernel model) is derived from hypotheses about ecological factors affecting space use (Horne and Garton, 2006). For each of these analyses, we determined 95%, 50%, and core (e.g., 30 – 40% isopleths) home-range estimates and used the ASU Arc-GIS v.1 extension (Carpenter, 2009) to import the ASU output into Arc-GIS v.9.3 to view and delineate the area for each home-range utilization distribution (Fig. 1). To permit comparisons of our home-range estimates to other studies, we used Hawth's Tools v.3.27 (Beyer, 2004) for Arc-GIS to estimate home-ranges via the minimum convex polygon (MCP) method (Fig. 1). We compared differences in home-range estimates (MCP, core UD, 50% UD, and 95% UD) between male and gravid female snakes and between males monitored in closed canopy (Control and Burn) and open canopy (Thin and Thin with Burn) stands using an independent samples *t*-test. In terms of evaluating treatment effects on home-range size, we limited comparisons to closed and open canopy stands because we lacked adequate home range estimates to evaluate individual treatment effects. Statistical significance was determined at an alpha level of 0.05.

2.4. Habitat use

2.4.1. Macrohabitat analysis

We evaluated macrohabitat use (use of habitats at the home-range scale) patterns at the core and 95% utilization distribution home range scales. To identify the area of available habitat within each of these spatial scales, we buffered each snake location by the average 95% utilization distribution area (males–17.8 ha; gravid females–7.1 ha) and average core utilization distribution area (males–2.1 ha; females–0.8 ha) using ArcGIS 9.3. We used Hawth's Tools v.3.27 for ArcGIS (Beyer, 2004) to generate random points (i.e., 21 – 33 points for each snake) equal to the number of radiotelemetry points for home-range estimation within each snakes' buffered home-range to represent available habitat. We used aerial photographs (1 m^2 spatial resolution) collected in 2006 and 2009 to identify and classify forest stand conditions of the study area prior to and after forest management, respectively. We used these geospatial data layers to identify macrohabitat features (Table 1) at used and available (random) points. First, we used landscape classifications in the 2006 National Landcover Classification Dataset (Fry et al., 2011) to determine primary landscape (e.g., Mixed Forest, Pine Forest, Agriculture, Scrub/Shrub) categories. Additional landscape habitat categories not explicitly described in the NLCD were delineated from the NLCD and aerial photographs and included Thinned Forest, Hard Edge, Soft Edge, and Southern Pine Beetle habitats (described in Table 1) to further define macrohabitat use by *A. contortrix* throughout the study area. Because Agriculture and Scrub/Shrub habitats were minimally

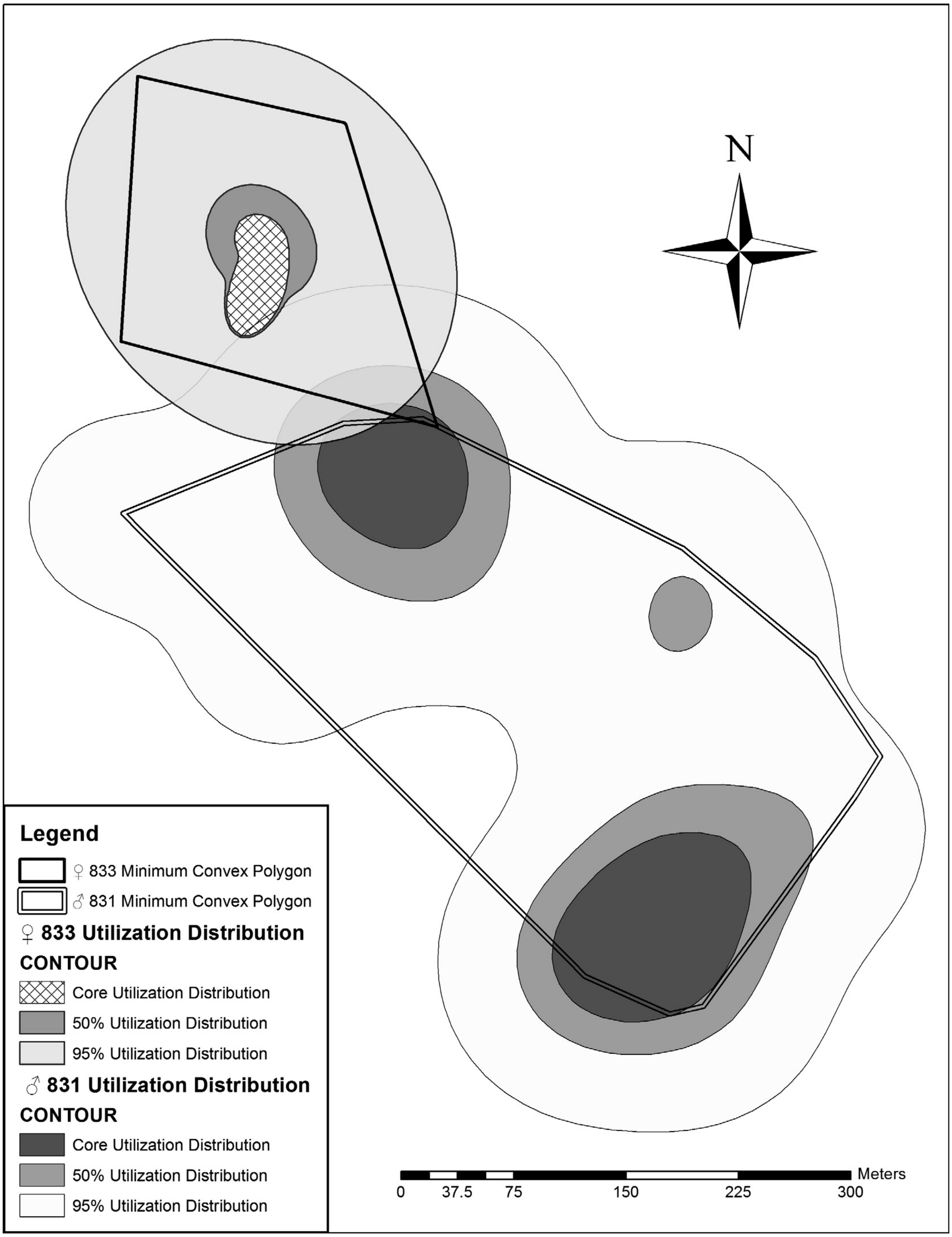

Fig. 1. Example home-range estimates for a male (snake 831) and gravid female (snake 833) *A. contortrix* in the William B. Bankhead National Forest. The dark (snake 833) and light with black-bordered (snake 831) polygons represent Minimum Convex Polygon home range estimates, whereas the three-toned concentric circular polygons represent the 95%, 50%, and core utilization distributions for snake 831 (adaptive Kernel utilization distribution) and snake 833 (two-mode bivariate normal mix utilization distribution). Home-ranges for both snakes were developed based on spatial data collected weekly from May – November.

represented (e.g., <1% of available habitats), we did not include these landscape classifications in further analyses. In addition, we did not include prescribed burning as one of the macrohabitat components evaluated during this study because burned areas within stands tended to be patchy and were impossible to differentiate via spatial data. We used compositional analysis (e.g., Aebischer et al., 1993; Richardson et al., 2006) via Multiple Analysis of Variance in SPSS v.24.0 (SPSS, 2016) to evaluate macrohabitat selection patterns at each home range scale for males and gravid females. We did not include data from non-gravid females in any habitat analyses because only one individual was monitored throughout the study.

2.4.2. Microhabitat analysis

We assessed microhabitat use patterns through a use-availability approach, whereby occupied locations were compared directly to a random and potentially unused location (Compton et al., 2002; Harvey and Weatherhead, 2006). Random locations were established by determining a random bearing (0°–360°) and distance (1–50 m) determined from each snake location. At each

Table 1
Descriptions of macrohabitat types used and available for use by radiotracked Copperheads (*Agkistrodon contortrix*) in the William B. Bankhead National Forest, Alabama, U.S.A.

Macrohabitat type[a]	Macrohabitat description
Mixed Forest (MF)	Forests composed of a broad mixture of deciduous tree species, with interspersed evergreen tree species
Pine Forest (PF)	Unmanaged pine forests dominated by Virginia Pine (*Pinus virginiana*) or Loblolly Pine (*P. taeda*)
Thinned Forest (TF)	Forest stands that have been thinned through silvicultural means. Heavy Thin and Light Thin treatments were combined in this macrohabitat category.
Southern Pine Beetle (SP)	Forest stands disturbed by infestations of the Southern Pine Beetle (*Dendroctonus frontalis*)
Hard Edge (HE)	An abrupt interface between forest and an open habitat, specifically roads and fields. We used a buffer of 15 m to classify use of a Hard Edge as recommended in Blouin-Demers and Weatherhead (2001)
Soft Edge (SE)	The interface between intact forest and Thinned Forest. We used a 15 m buffer to classify use of a soft edge as recommended in Blouin-Demers and Weatherhead (2001)

[a] Habitats within the study area were characterized using aerial photographs along with Southern Pine Beetle forest stand shapefiles supplied by the USDA Forest Service.

Table 2
Microhabitat variables assessed at each used and random (available) site for radiotracked Copperheads (*Agkistrodon contortrix*) in the William B. Bankhead National Forest, Alabama, U.S.A.

Habitat variable	Abbreviation	Habitat variable description
Assessed inside of 1 m^2 grid		
Percent litter	%_Litt	Forest litter cover (%) within a 1 m^2 grid. Variable had to occupy one grid cell to be counted
Percent woody	%_Wood	Woody stem cover (%) within a 1 m^2 grid. Variable had to occupy one grid cell to be counted
Percent CWD	%_CWD	Coarse Woody Debris (CWD) cover (%) within a 1 m^2 grid. Variable had to occupy one grid cell to be counted
Percent slash	%_Slash	Slash cover (%) within a 1 m^2 grid. Variable had to occupy one grid cell to be counted
Percent rock	%_Rock	Rock cover (%) within a 1 m^2 grid. Variable had to occupy one grid cell to be counted
Forest level 1	For_1	Average understory tree cover (%) taken at each of four points along the 1 m^2 grid
Forest level 4	For_4	Average canopy tree cover (%) taken at each of four points along the 1 m^2 grid
Litter depth	L_depth	Average litter depth (cm) taken at each of four points along the 1 m^2 grid
Canopy cover	Can_cov	Average canopy cover (%) take at each of four points along the 1 m^2 grid
Number of woody stems	No_ws	Number of woody stems within the 1 m^2 grid
Air temperature snake	AT_snake	Air temperature (°C) taken within 10 cm of the snake
Relative humidity snake	RH_snake	Relative humidity (%) taken within 10 cm of the snake
Soil temperature	T_soil	Soil temperature (°C) taken within 10 cm of the snake
Assessed outside of 1 m^2 grid		
Basal area	Bas_area	Cross-sectional area (m^2/ha) of living overstory trees surrounding each sampled plot. Determined with a 10 power prism
Percent pine	Per_pine	Composition (%) of overstory pine tree species. Limited to trees tallied in the basal area estimate
Nearest log distance	N_logd	Distance (cm) to nearest log $\geq$ 10 cm in diameter to plot center. Log could not be within 1 m^2 grid
Log volume	Log_vol	Volume (m^3) to nearest log $\geq$ 10 cm in diameter to plot center. Determined as volume of a cylinder: π $r^2 \times$ length
Nearest rock distance	Rock_d	Distance (cm) to nearest rock $\geq$ 10 cm in diameter to plot center. Rock could not be within 1 m^2 grid

used and random location, we used a 1 m^2, 10 × 10 grid to describe the microhabitat sites used by *A. contortrix* similar to other studies and as recommended in Reinert (1984a,b), Harvey and Weatherhead (2006), Table 2. We placed the center of the 1 m^2 quadrat at the location of each snake and random site surveyed. We used the sampling grid to estimate percent cover of litter, woody vegetation, coarse-woody-debris (CWD), slashpiles, rock, and other microhabitat variables as described in Table 2.

Microclimatic variables (air temperature and relative humidity) were measured at used and random locations immediately after a snake was located during a tracking event. We returned to the used and random locations approximately 1 – 3 weeks later to measure the remaining microhabitat variables in Table 2. We delayed microhabitat surveys until a snake had vacated a selected site to avoid additional disturbance to the radiotracked individual. Habitat plot data were collected from early May through late August for each year of the study. We completed a microhabitat assessment only when a snake was confirmed to be above ground and had moved at least 1 m from a previous location.

2.5. Statistical analysis

We developed seven microhabitat and microclimate (habitat hereafter) models based on variables supported in habitat use studies of other pit-viper species (e.g., Cross and Peterson, 2001; Harvey and Weatherhead, 2006; Reinert, 1984a,b; Steen et al., 2012) and from our biological knowledge of the study organism (Table 3). We used a mixed-models approach for all analyses to account for non-independence of microhabitat samples for individual snakes (random effect).

We developed three analyses to evaluate the individual effects of snake sex and forest treatment on microhabitat use, including two sex-based analyses and one treatment-based analysis. For the analyses that evaluated the effect of snake sex on microhabitat use, we used generalized linear mixed models (GLMMs) via the lme4 package (Bates et al., 2015) in R v.3.3.0 (R Core Team, 2016). We created a binary dataset where (1) represented a "used" site and (0) represented an "unused", random site. We tested the difference among used and random sites based on a binomial distribution and logit link function. For the analysis that examined microhabitat use differences among forest treatments, we only used data from male *A. contortrix* locations because we did not have sufficient data to test forest treatment effects for female snake habitat use. We collated each of the two thin and thin with burn treatments into thin and thin with burn groups, respectively to maximize statistical power. We subtracted microhabitat and microclimate data collected at each random habitat point from each of the respective paired snake locations to create a dataset representing relative difference among used and random sites. We used the lmer function in the lme4 package (Bates et al., 2015) in R v. 3.3.0 (R Core Team, 2016) to test effects of forest treatment on male snake microhabitat use.

We used Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$; Burnham and Anderson, 2002) to evaluate

Table 3
A-priori habitat models developed to test for microhabitat use differences between used and random microhabitat sites for male and gravid female *A. contortrix* among differently managed forest stands (i.e., Control, Burn, Thin, and Thin with Burn). Refer to Table 2 for associated microhabitat and microclimate variable abbreviations.

Microhabitat model	Variables
Climate	AT_Snake + RH_Snake + T_soil
Cover depth	L_depth + %_CWD + %_Slash
Forest structure	Bas_Area + Can_cov + Per_pine
Groundcover	%_Litt + %_Woody + %_CWD + %_Rock + %_Slash
Vertical structure	T_ws + For_1 + For_4
Thermoregulation	Can_cov + AT_Snake + T_soil
Woody debris	% _CWD + N_CWDdist + N_CWDvol
Global	AT_Snake + RH_Snake + T_soil + L_depth + Bas_Area + Can_cov + Per_pine + %_Litt + %_Woody + %_CWD + %_Rock + %_Slash + T_ws + For_1 + For_4 + N_CWDdist + N_CWDvol

candidate habitat models and select the most parsimonious model that best explained *A. contortrix* habitat use. We evaluated each of the habitat models (Table 3) and calculated AIC_c and ΔAIC_c as recommended in Burnham and Anderson (2002). Akaike weights (ω_i) were calculated from ΔAIC_c values to evaluate the evidence that a particular hypothesis was the most parsimonious model. We examined evidence ratios to evaluate the degree of difference between the highest-supported models with evidence ratios < 2.7 (Burnham and Anderson, 2002). We calculated parameter estimates for candidate models with greatest support and used Akaike's weights along with parameter estimates to calculate 95% confidence intervals (Burnham and Anderson, 2002).

3. Results

We recorded 766 individual locations from 30 *A. contortrix* over the course of this study (Table 4). The number of observations per snake ranged from 6 (5 weeks) to 53 (13 months) total observations per snake (Table 4). Five snakes were depredated during this study, whereas four snakes were lost due to transmitter failure and one snake died one month after surgery implantation (Table 4). Overall, we sampled microhabitat features at 432 (males–378; gravid females–54) snake locations and at 432 random locations.

3.1. Home-range analysis

We calculated home-ranges for 22 snakes (16 males, 5 gravid females, and 1 non-gravid female) that were radio-tracked throughout a majority of the active season (March – November). The fixed kernel home-range procedure was identified as the best home-range estimation technique for 11 snakes, whereas the adaptive kernel was selected as the best estimation procedure for 5 snakes (Table 5). The two-mode bivariate normal mix, two-mode bivariate circle, and one-mode bivariate normal utilization were each identified twice as the best home-range utilization distribution estimation technique (Table 5).

We detected differences in home-range size between male and gravid female snakes. Males had larger home-range sizes than gravid females for 95% utilization distributions (males 17.8 ± 2.3 ha; females 7.1 ± 1.8 ha; $t_{19} = 2.49$; $p = 0.023$), 50% utilization distributions (males 3.9 ± 0.6 ha; females 1.0 ± 0.4 ha; $t_{19} = 2.687$; $p = 0.012$), core area utilization distributions (males 2.1 ± 0.3 ha; females 0.8 ± 0.3 ha; $t_{19} = 2.687$; $p = 0.015$), and 100% minimum convex polygons (males 12.0 ± 1.9 ha; 4.1 ± 1.1 ha;

Table 4
Summary of total radiotracked Copperheads (*Agkistrodon contortrix*) monitored from April 2006 – November 2008 in the William B. Bankhead National Forest, Alabama, U.S.A. Please refer to the footnotes for specific explanations of snake number symbols.

Snake number	Sex[a]	Treatment type	# of locations	Tracking period	Final result
133[*,†]	M	Thin	27	8/18/2006 – 9/4/2007	Survived
133J[*,†]	M	Thin with burn	30	5/6/2008 – 11/10/2008	Survived
134[*,†]	M	Burn	29	8/21/2006 – 8/27/2007	Survived
134B[†]	M	Control	14	5/9/2008 – 8/1/2008	Depredated (unknown predator)
135[*,†]	M	Thin with burn	28	8/23/2006 – 9/4/2007	Survived
135C[*,†]	M	Thin	29	5/9/2008 – 11/10/2008	Survived
136[*,†]	M	Thin	28	8/23/06 – 9/4/2007	Survived
136T[*,†]	M	Thin	29	5/16/2008 – 11/10/2008	Survived
137[*,†]	M	Thin with burn	42	5/8/2007 – 9/29/2008	Survived
423[*,†]	M	Thin with burn	37	5/17/2007 – 9/2/2008	Transmitter signal lost (fate unknown)
424[*,†]	M	Thin with burn	40	5/19/2007 – 9/26/2008	Survived
426[†]	M	Control	15	6/3/2007 – 9/22/2008	Depredated (unknown predator)
427	M	Thin with burn	6	6/9/2007 – 7/17/2007	Depredated (unknown predator)
428[†]	M	Thin	9	6/23/2007 – 8/16/2007	Depredated (unknown predator)
429[*,†]	M	Thin with burn	33	7/23/2007 – 9/29/2008	Survived
430[†]	M	Thin	20	7/23/2007 – 7/9/2008	Depredated (unknown predator)
831[*,†]	M	Thin	45	5/17/2006 – 8/28/2007	Survived
833S[*,†]	M	Thin with burn	27	5/23/2008 – 11/10/2008	Survived
834[*,†]	M	Control	35	7/7/2006 – 9/2/2007	Survived
835[†]	M	Thin	10	7/27/2006 – 9/21/2006	Depredated (black kingsnake)
836[*,†]	M	Control/burn	53	4/22/2006 – 9/11/2007	Survived
837[*,†]	M	Control	31	4/29/2006 – 10/27/2006	Transmitter removed the following spring
840[†]	M	Control	13	8/10/2006 – 6/14/2007	Survived
425[*,†]	F(G)	Thin with burn	21	5/20/2007 – 11/2/2007	Transmitter signal lost (fate unknown)
425[*]	F(NG)	Thin with burn	21	4/30/2008 – 9/2/2008	Transmitter signal lost (fate unknown)
503[*,†]	F(G)	Thin with burn	30	5/9/2008 – 11/10/2008	Survived
504[*,†]	F(G)	Thin	27	5/31/2008 – 11/10/2008	Survived
832	F(Unk)	Control	8	4/29/2006 – 6/4/2006	Died (incision site opened)
833[*,†]	F(G)	Thin	42	5/23/2006 – 6/14/2007	Depredated (unknown predator)
834B[*,†]	F(G)	Thin	21	6/29/2008 – 11/10/2008	Survived
838	F(Unk)	Control/burn	8	5/27/2006 – 7/7/2006	Transmitter signal lost (fate unknown)

[a] M- male, F- female, G-gravid, NG-nongravid, and Unk-unknown reproductive condition.

[*] Individuals used for home-range and macrohabitat scale use estimation.

[†] Habitat data from these individuals was used to evaluate microhabitat use.

Table 5
Home-range estimates (utilization distributions [UD]) for radiotracked Copperheads (*Agkistrodon contortrix*) in the William B. Bankhead National Forest, Alabama, U.S.A. (2006–2008). Home-range estimates were determined for individuals monitored for a majority of the active season (April – November).

Snake number[a]	Gender	Treatment type	Number of locations	Home range method[b]	95% UD (ha)	50% UD (ha)	Core UD (ha)	MCP (ha)[c]
133	M	Thin	27	FK	18.7	3.9	2.1	23.8
133J	M	Thin with burn	30	FK	16.8	4.1	2.3	7.7
134	M	Burn	29	FK	6.6	1.3	0.8	4.6
135	M	Thin with burn	28	FK	19.8	4.5	2.3	14.9
135C	M	Thin	29	FK	43.7	10.9	5.4	28.9
136	M	Thin	28	TBNM	17.1	4.2	2.3	17.6
136T	M	Thin	29	FK	20.0	4.4	2.4	8.5
137	M	Thin with Burn	26	TBC	13.2	2.3	1.7	8.5
423	M	Thin with burn	22	FK	15.6	3.9	1.9	7.0
424	M	Thin with burn	25	OBN	8.3	1.9	1.1	3.8
429	M	Thin with burn	26	AK	9.2	1.9	1.1	3.9
831	M	Thin	32	AK	20.1	4.6	2.3	10.3
833S	M	Thin with burn	27	OBN	15.0	3.5	1.9	9.9
834	M	Control	28	FK	19.7	3.9	2.1	12.9
836	M	Control/burn	33	FK	8.9	2.1	1.1	7.2
837	M	Control	31	AK	31.4	5.2	3.2	22.0
425	F(G)	Thin with burn	21	FK	11.3	2.7	1.6	3.2
425	F(NG)	Thin with burn	21	TBC	29.7	1.7	1.5	12.7
503	F(G)	Thin with burn	30	AK	9.3	0.9	0.8	5.0
504	F(G)	Thin	27	AK	8.4	1.0	1.0	7.9
833	F(G)	Thin	27	TBNM	5.5	0.5	0.3	3.2
834B	F(G)	Thin	21	FK	0.8	0.1	0.1	1.4

[a] Please refer to Table 4 for number of locations and time period that a snake was tracked with radiotelemetry.
[b] Evaluated using the Animal Space Use program (Horne and Garton, 2006); AK – Adaptive Kernel, FK – Fixed Kernel, OBN – One-mode Bivariate Normal, TBC – Two-mode Bivariate Circle, TBNM – Two-mode Bivariate Normal Mix.
[c] Evaluated using Hawth's Tools v.3.27 for ArcGIS (Beyer, 2004).

Table 6
Macrohabitat use versus availability for Copperheads (*Agkistrodon contortrix*) in the William B. Bankhead National Forest (2006–2008). Please refer to the methods section for specific descriptions of how 95% and core area utilization distributions were used to determine availability of macrohabitats described in Table 1. Habitats that share a common underline were preferred equally.

Home-range scale	N	Mixed Forest (MF)	Pine Forest (PF)	Thinned Forest (TF)	Southern Pine Beetle (SP)	Hard Edge (HE)	Soft Edge (SE)	Used ↔ avoided	Statistics		
95% area UD[a]									Λ[c]	F	p
Male snakes	16	54.8/58.7	5.4/12.3	11.6/12.4	13.1/4.0	13.0/2.5	2.0/10.1	HE SP MF TF PF SE	0.15	12.20	<0.001
Gravid females	5	55.9/70.5	0.0/1.9	30.2/9.7	6.7/0.9	0.7/4.3	6.5/12.6	TF SP MF PF HE SE	0.003	97.27	0.08
Core area UD[b]											
Male snakes	16	54.8/55.9	5.4/9.3	11.6/14.6	13.1/6.6	13.0/5.0	2.0/8.6	HE SP MF PF TF SE	0.26	6.40	0.005
Gravid females	5	55.9/56.7	0.0/2.3	30.2/14.9	6.7/4.5	0.7/1.5	6.5/20.1	TF MF HE SP PF SE	0.18	1.14	0.60

[a] Represents area within average 95% utilization distribution.
[b] Represents area within average core utilization distribution.
[c] Wilk's lambda.

$t_{19} = 2.251$; $p = 0.036$). The one non-gravid female had home-range estimates larger than gravid females and more similar to males in this study (Table 5). In addition to having smaller core area estimates, gravid females usually had one centralized activity area, whereas males had more than one activity center. Anecdotally, we noted that male snakes made a series of continuous movements throughout the active season, whereas gravid females generally settled on a location for gestation and parturition by June. We did not detect an effect of thinning on male home-range size for 95% utilization distributions (closed canopy 16.7 ± 5.7 ha; open canopy 18.1 ± 2.6 ha; $t_{14} = 0.268$, $p = 0.793$), 50% utilization distributions (closed canopy 3.1 ± 0.9 ha; open canopy 4.2 ± 0.7 ha; $t_{14} = 0.817$, $p = 0.427$), core area utilization distributions (closed canopy 2.2 ± 0.3 ha; open canopy 1.8 ± 0.5 ha; $t_{14} = 0.687$, $p = 0.503$), and 100% minimum convex polygons (closed canopy 12.2 ± 2.2 ha; open canopy 11.7 ± 3.9 ha; $t_{14} = 0.087$; $p = 0.932$).

3.2. Macrohabitat selection

We detected a difference in male macrohabitat use at the 95% ($\lambda = 0.15$; $F_{15} = 12.2$; $p < 0.001$) and core utilization distribution ($\lambda = 0.26$; $F_{15} = 6.40$; $p = 0.005$) scales (Table 6). Specifically, males used Hard-Edge and Southern Pine Beetle macrohabitats greater than their availability across the landscape at both utilization distribution home-range scales (Table 6). Soft Edge, Pine Forest, and Thinned Forest macrohabitats were the least used macrohabitat types by male snakes based on availability of these habitats (Table 6). Although gravid females tended to use Thinned Forest and Southern Pine Beetle macrohabitats greater than what was available, this trend was not statistically significant at the 95% ($\lambda = 0.003$; $F_4 = 97.27$; $p = 0.08$) and core ($\lambda = 0.25$; $F_4 = 9.41$; $p = 0.60$) utilization distribution scales (Table 6). We observed that three out of the five gravid females used Thinned Forest, whereas

Table 7
Microhabitat model evaluation results based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c). Model results include comparisons of used and random (available) microhabitat sites for male and gravid female Copperheads (*A. contortrix*) and microhabitat use differences for male *A. contortrix* in differently managed forest stands (Control, Burn, Thin, and Thin with Burn) in the William B. Bankhead National Forest (Alabama).

Model set	Model	−2 LL[a]	K[b]	AIC_c[c]	ΔAIC_c[d]	ω_i[e]
Male *A. contortrix* habitat	Global	668.0	19	746.11	0.00	0.99
Female *A. contortrix* habitat	Cover Depth	111.8	5	132.99	0.00	0.99
Male *A. contortrix* treatment	Climate	1295.2	6	1319.45	0.00	0.99

[a] Value derived from paired logistic regression output.
[b] Number of parameters in each model.
[c] Akaike's information criterion adjusted for small samples.
[d] The difference between the best supported AIC model and each candidate model.
[e] Akaike's weight value indicates relative weight of each model. Higher values indicate models with better support.

the other two females were observed anecdotally to use forested habitat with canopy gaps created through windthrow of *Quercus* species.

3.3. Microhabitat selection

In the sex-based microhabitat analysis, we detected differences in microhabitat use patterns between male and gravid female snakes. For male snakes, the Global model had greatest support ($AIC_c = 746.11$; $\omega_i = 0.99$; Table 7). Within this model, percent CWD and litter depth variables were positively-associated with occupied microhabitat sites, whereas percent pine, forest level 4 (average percent canopy tree cover), and percent litter variables were negatively-associated with *A. contortrix* microhabitat use (Fig. 2). Within this model, relative support was greatest for litter depth ($\beta = 1.65 \pm 0.16$; 95% C.I.: 1.35–1.96), percent litter ($\beta = -0.80 \pm 0.13$; 95% C.I.: −1.06 to −0.54), and percent CWD ($\beta = 0.56 \pm 0.14$; 95% C.I.: 0.30–0.83) compared to other variables contained in this model (Table 8). For gravid female snakes, the Cover Depth model had highest support ($AIC_c = 132.99$; $\omega_i = 0.99$). Within this model, litter depth and percent CWD variables were positively-associated with used microhabitat sites for gravid

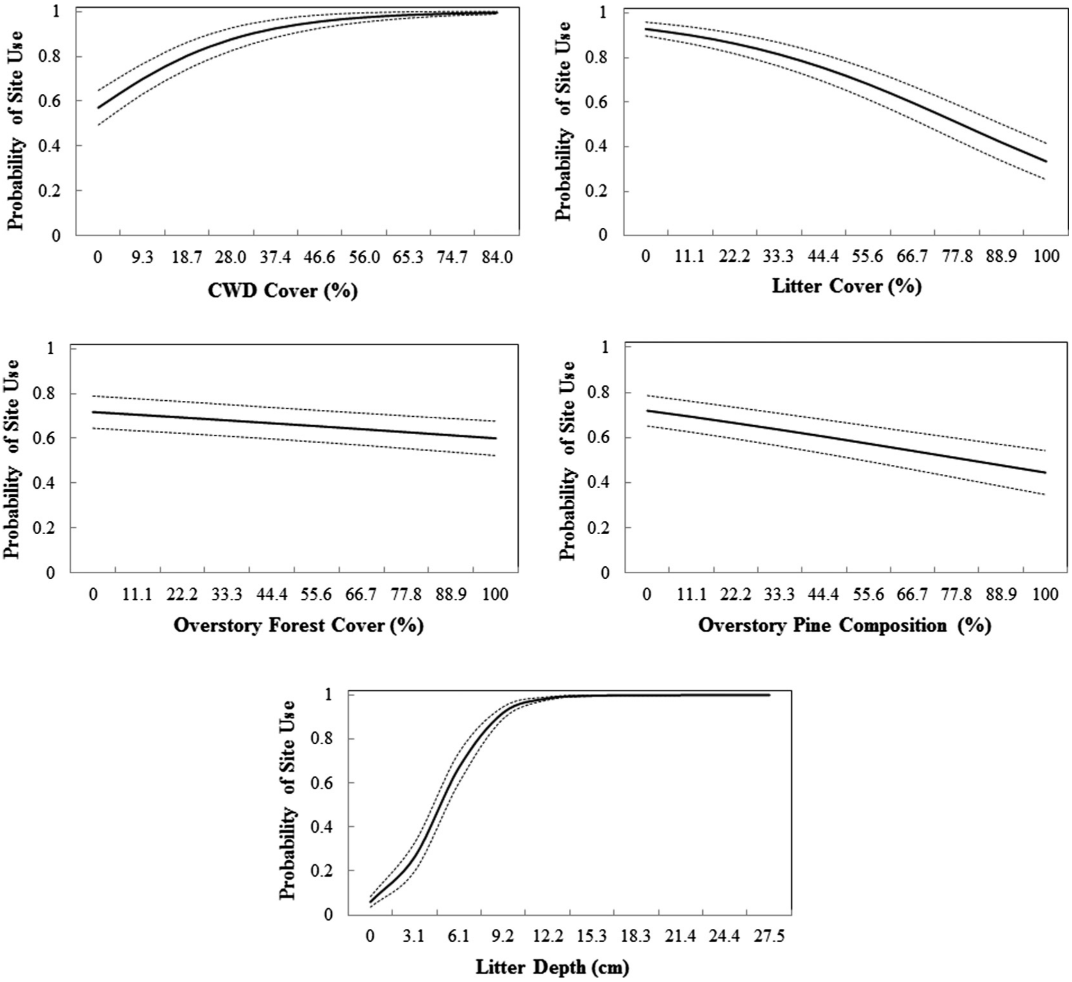

Fig. 2. Predicted probability of microhabitat use by male *A. contortrix* based on Generalized Linear Mixed Model results. Predicted responses of variables were plotted based on the highest-supported model describing microhabitat use, which was the Global model. Please refer to Table 3 for a description of habitat models that were evaluated. Dotted lines on either side of the fitted response represent standard errors.

Table 8
Standardized β-coefficients, standard errors, and 95% confidence intervals for habitat variables included in the highest supported habitat model (Global model) for male *A. contortrix*. Variables listed in bold had confidence intervals that did not overlap zero.

Variable	β-coefficient	S.E.	95% C.I.
AT_snake	−0.20	0.31	−0.81 to 0.41
RH_snake	−0.15	0.15	−0.45 to 0.14
T_soil	0.08	0.12	−0.16 to 0.33
%_CWD	**0.56**	**0.14**	**0.30 to 0.83**
n_CWDvol	−0.16	0.09	−0.35 to 0.02
n_CWDdist	−0.03	0.10	−0.22 to 0.17
%_Litt	**−0.80**	**0.13**	**−1.06 to −0.54**
%_Rock	0.20	0.13	−0.05 to 0.46
%_Woody	−0.09	0.10	−0.28 to 0.09
%_Slash	3.09	1.88	−0.60 to 6.77
Bas_area	−0.07	0.13	−0.31 to 0.18
Can_cov	0.22	0.12	−0.02 to 0.46
%_pine	**−0.36**	**0.11**	**−0.58 to −0.14**
For_1	−0.08	0.11	−0.30 to 0.14
For_4	**−0.23**	**0.11**	**−0.44 to −0.02**
No_ws	0.04	0.12	−0.19 to 0.27
L_depth	**1.65**	**0.16**	**1.35 to 1.96**

Table 9
Standardized β-coefficients, standard errors, and 95% confidence intervals for habitat variables included in the highest supported microhabitat model (Cover Depth model) for gravid female *A. contortrix*. Variables listed in bold had confidence intervals that did not overlap zero.

Variable	β-coefficient	S.E.	95% C.I.
%_CWD	**1.07**	**0.38**	**0.33 to 1.81**
%_Slash	−0.33	0.68	−1.67 to 1.01
L_depth	**1.20**	**0.44**	**0.34 to 2.06**

Table 10
Standardized β-coefficients, standard errors, and 95% confidence intervals for treatment effects of the highest supported microhabitat model (Climate model) for male *A. contortrix*. Variables listed in bold had confidence intervals that did not overlap zero.

Variable	β-coefficient	S.E.	95% C.I.
Burn	−0.28	0.37	−1.01 to 0.45
Thin	**−0.74**	**0.25**	**−1.23 to −0.25**
Thin with burn	−0.79	0.41	−1.59 to 0.01

females (Fig. 3). Support was relatively greater for litter depth ($\beta = 1.20 \pm 0.44$; 95% C.I.: 0.34–2.06) compared to percent CWD ($\beta = 1.07 \pm 0.38$; 95% C.I.: 0.33–1.81) for describing microhabitat use of gravid female snakes relative to random sites (Table 9).

For the analysis that evaluated forest treatment effects on microhabitat use of male *A. contortrix*, we found greatest support for the Climate microhabitat model ($AIC_c = 1395.45$; $\omega_i = 0.99$; Table 7). Specifically, we found support for this model to differentiate microhabitat use between used and random sites for *A. contortrix* radiotracked in thin-only stands ($\beta = -0.74 \pm 0.25$; C.I.: −1.23 to −0.25; Table 10). Specifically, air and soil temperature measurements were 1.07 ± 0.37 °C and 0.76 ± 0.18 °C lower, respectively at used compared to random microhabitat sites for *A. contortrix* radiotracked in thin-only forest stands (Fig. 4). Although confidence intervals overlapped zero, we detected relatively high support for the Climate model describing differences in microhabitat use in thin with burn stands ($\beta = -0.79 \pm 0.41$; C.I.: −1.59 to 0.01; Table 10). We did not detect an effect of forest treatment for relative humidity measurements between used and random microhabitat sites among the forest treatments.

4. Discussion

Our study provides support for multi-scale habitat selection in *A. contortrix*, but use differed by sex and female reproductive condition. We detected macrohabitat use patterns for male *A. contortrix* at the 95% home-range utilization distribution scale. Male snakes used Hard Edge and Southern Pine Beetle macrohabitats greater than their availability and avoided Pine Forest and Cut Forest. Male snakes primarily used Hard Edge macrohabitats at the interface between forest and open fields (i.e., cultivated game fields) and along trail and forest road edges. Snakes may use edge habitats due to increased thermoregulation opportunities and may capitalize on opportunistic prey encounters (Blouin-Demers and Weatherhead, 2001; Carfagno and Weatherhead, 2006; Carfagno et al., 2006; Row and Blouin-Demers, 2006; Sperry and Weatherhead, 2009). Some species of colubrid snakes are major predators of avian species (Carfagno et al., 2006) and represent one of the largest sources of nesting bird mortality (Thompson et al., 1999; Weatherhead and Blouin-Demers, 2004). However, Weatherhead et al. (2010) suggest that the apparent increased predation of nesting birds in edge habitats is due to relatively higher snake densities in these habitats rather than snakes selecting these habitats exclusively to target avian prey. Snakes may also use edge habitats due to abundance of refuge sites (e.g., tree blow-downs) at the field/forest edge interface (Waldron et al., 2006).

Male snakes also used Southern Pine Beetle macrohabitats disproportionate to their availability in the study area. This was likely due to the increased availability of cover (i.e., large fallen logs) and thermoregulation sites (i.e., large canopy gaps). Infestations by the Southern Pine Beetle often result in large numbers of downed trees, thereby increasing the abundance of fallen logs and large canopy gaps (Duncan and Linhoss, 2005; Knebel and Wentworth, 2007). *Agkistrodon contortrix* may also display increased use of Southern Pine Beetle macrohabitats due to increased prey density. Forest stands with abundant CWD cover often have greater

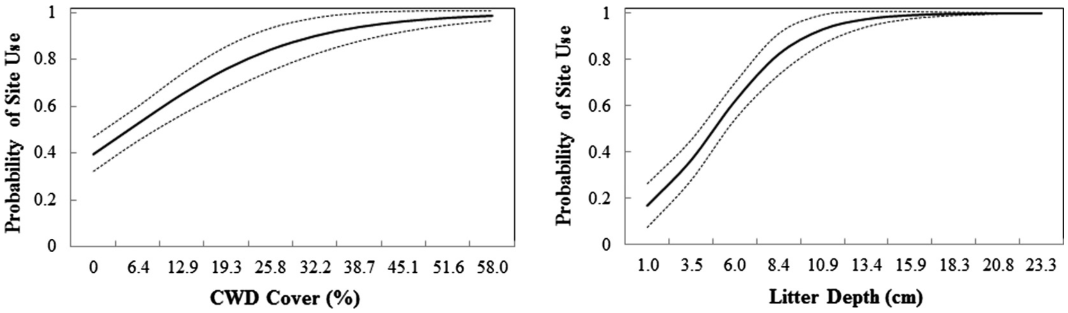

Fig. 3. Predicted probability of microhabitat use by gravid female *A. contortrix* based on Generalized Linear Mixed Model results. Predicted responses of variables were plotted based on the highest-supported model describing microhabitat use, which was the cover depth model. Please refer to Table 3 for a description of habitat models that were evaluated. Dotted lines on either side of the fitted response represent standard errors.

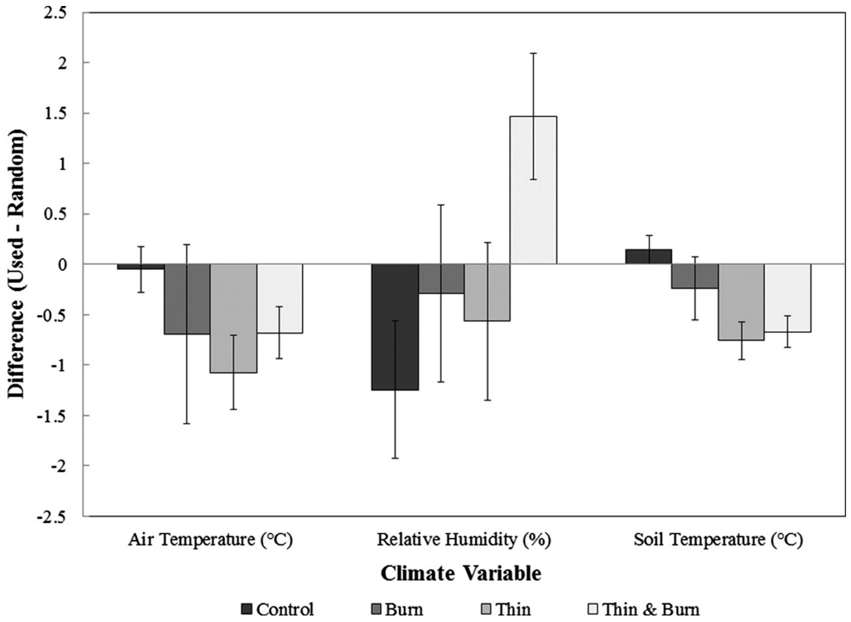

Fig. 4. Mean differences between microclimate variables at "used" and "unused" microhabitat locations for male *A. contortrix* in differently-managed forest stands (Control, Burn, Thin, and Thin with Burn) in the William B. Bankhead National Forest, U.S.A. (2006 – 2008). Mean differences for air temperature, soil temperature, and relative humidity variables were plotted based on the highest-supported model describing microhabitat use by treatment, which was the Climate model. Please refer to Table 3 for a description of habitat models that were evaluated.

densities of small mammalian prey compared to habitats that lack woody debris (Loeb, 1999; McKay and Komoroski, 2004). As further evidence, Sperry and Weatherhead (2010) demonstrated that manmade brush piles created after stand disturbances led to increased use by both snakes and mammalian prey.

Although statistically-significant habitat use patterns were not observed for gravid females at the macrohabitat scale, these snakes tended to concentrate activity in areas with canopy disturbances. Three of these snakes moved into thinned stands, whereas two snakes moved into areas with canopy gaps caused by windthrow of late seral stage *Quercus* species. Gravid female snakes of other species have been found to use open macrohabitats with greater thermoregulation opportunities (Crane and Greene, 2008; Harvey and Weatherhead, 2006; Marshall et al., 2006), which are important during embryogenesis (Crane and Greene, 2008; Foster et al., 2009). Unfortunately, the sample size for gravid females in our study was low, which undoubtedly influenced the statistical power of the macrohabitat use analyses. We did not include the one non-gravid female into habitat analyses due to low sample size, but space use patterns along with personal observations indicate that the non-gravid female was more similar to males in their space and habitat use patterns compared to the other gravid females.

Microhabitat comparisons indicated that both male and gravid female snakes used microhabitats that possessed relatively greater litter depth and CWD cover. Male *A. contortrix* in the northeastern United States have been found to select microhabitats with abundant CWD cover (Cross and Peterson, 2001), whereas gravid females tend to select open sites with abundant rock cover (Reinert, 1984a). Although male and gravid female *A. contortrix* selected microsites with similar habitat attributes in this study, we suggest they selected these habitats for different reasons. Male *A. contortrix* likely selected these sites as optimal prey ambush sites, whereas gravid females selected sites for protection from potential predators during embryogenesis and parturition. Male and non-gravid female Timber Rattlesnakes (*Crotalus horridus*) have been found to use logs and other downed woody debris as prey ambush sites. Moreover, forest small mammals use logs and other CWD as runways and sit-and-wait predators can capitalize on the increased chance of capturing prey at these sites (Reinert et al., 1984). Gravid *C. horridus* along with other gravid pitviper species do not commonly feed during parturition (Reinert et al., 1984), which suggests that gravid females in our study were likely using selected microsites to benefit parturition rather more so than for foraging opportunities. The proclivity for gravid pit-vipers to use open habitats is well documented and these individuals select these habitats for protection from predators and increased thermoregulation opportunities (Marshall et al., 2006; Reinert, 1984a).

We used a unique information-theoretic approach to generate home-range estimates for individual snakes based on the fit of the data rather than choosing a single technique based solely on use in the published literature as this method is more likely to represent biologically-founded estimates (Horne and Garton, 2006). The estimated home-range values in our study were larger than those determined by Fitch and Shirer (1971). The range of 3–9 ha reported by Fitch and Shirer (1971) likely under represents total home-range as study snakes were force-fed transmitters, which has been found to initiate post-feeding behaviors (e.g. preference for warm locations and sedentary behavior; Lutterschmidt and Reinert, 1990). Home-range estimates for *A. contortrix* from the northeastern United States ranged from 0.6 to 44.5 ha (Smith et al., 2009), which are relatively comparable to our home-range estimates. However, the largest snake home-range in Smith et al.'s study was nearly twice the size of the largest home-range that we observed (based on MCP estimate). As our study relied on an information-theoretic approach to select the appropriate utilization distribution home range estimation technique, direct comparisons with home range estimates from previous studies are limited. Snake home-range patterns are influenced by the spatial arrangement of hibernation, prey ambush, and parturition sites. For example, studies of the Eastern Massasauga Rattlesnake (*Sistrurus c. catenatus*) have reported home-range estimates that differ nearly threefold among study sites (Degregorio et al., 2011; Durbian et al., 2008; Johnson, 2000; Marshall et al., 2006; Reinert and Kodrich, 1982); these wide-ranging estimates are likely due to the spatial arrangement of biological resources, such as parturition and hibernation sites at a particular field site (Reinert and Kodrich, 1982; Seigel and Pilgrim, 2002).

In our study, male *A. contortrix* home-ranges were larger than gravid females at all home range scales evaluated. Male snakes tended to make a series of continuous movements throughout the active season and rarely settled on one site for more than two repeated locations. Gravid females generally made a series of relatively larger movements during the early spring and tended to settle on a permanent location around June and remained at this location until late August or early September. Similar patterns of reduced movements by gravid females have been noted by others (Degregorio et al., 2011; Marshall et al., 2006; Reinert and Kodrich, 1982; Reinert, 1984a,b) as home-range patterns in pit-vipers are highly dependent on reproductive condition, where males and non-gravid females exhibit larger home-ranges compared to gravid females (Johnson, 2000; Marshall et al., 2006; Waldron et al., 2006). Our sample size of non-gravid females was limited to one snake (tracked continuously throughout one full season), but this snake tended to make a series of large movements to and from the core area, similar to the male snakes monitored during this study. Larger sample sizes are necessary to make conclusions regarding spatial ecology and home-range size of non-gravid females, however our limited results agree with other studies on pitvipers (Harvey and Weatherhead, 2006; Johnson, 2000; Waldron et al., 2006).

We were unable to detect impacts of thinning on the home-range size of *A. contortrix*. We originally hypothesized that snakes in harvested stands would have larger home-ranges due to the decreased abundance of microhabitat cover sites. Most snakes that were originally captured in harvested stands did not consistently use thinned forest and used a wide variety of macrohabitats in the surrounding landscape, which was further supported by the macrohabitat use analyses. A forest management study conducted in Indiana evaluated the impacts of even-age (clear-cut and shelterwood management) management on spatial ecology of Timber Rattlesnakes (*Crotalus horridus*) and found little difference in home-range size and spatial movements among treatments and between pre- and post-treatment conditions (MacGowan et al., 2017). Research by Howey et al. (2016) found that Black Racers (*Coluber constrictor*) moved more frequently in control stands versus burn stands, which the authors attributed to greater availability of open habitats in recently burned stands. We observed in our study that when male and gravid female snakes moved into thinned stands, they often used large slash piles as cover sites. Managers should consider leaving behind slash and logs as cover for snakes and other wildlife, as a wide array of forest dwelling species have been found to use slash and other down woody debris as cover sites (Hassinger, 1989). Although we were unable to test for microhabitat differences for gravid females in control and thinned stands, three out of the five gravid female *A. contortrix* used microhabitats within the thinned stands for extended time periods. Active canopy removal (e.g., thinning) has been shown to improve habitat conditions for some reptile species (Webb et al., 2005), specifically in disturbance-prone ecosystems where canopy removal was used to restore historical habitat conditions (Pike et al., 2011). Inference from our study is quite limited because we were unable to track the same individuals for a full active season before and after the implementation of forest management. In future studies, researchers should work collaboratively with forest managers and timber crews to ensure that snake movement and habitat selection data can be collected before, during, and after forest management practices. Reinert et al. (2011) represents the only study that has followed snake microhabitat use and spatial ecology before, during, and after forest management. Future studies should use this example as a blueprint to design and implement manipulative studies that evaluate landscape disturbance impacts on snakes and other mobile vertebrates.

In our study, *A. contortrix* demonstrated patterns of habitat use at multiple spatial scales; however, this effect was only detectable for male snakes. Although male *A. contortrix* used Southern Pine Beetle and Hard Edge macrohabitats greater than availability, *A. contortrix* likely used these habitats due availability of suitable microhabitats (i.e., microhabitat locations with greater litter cover and CWD cover) within these macrohabitats. Gravid females did not display use patterns for one macrohabitat type, but tended to use microhabitats with suitable cover and thermoregulation attributes. Both males and gravid females appear to use microhabitats based on increased cover in the form of CWD and litter depth, whereas gravid females additionally sought out sites that likely possessed optimal thermoregulation opportunities. Similarly, Waldron et al. (2008) found that Eastern Diamondback Rattlesnakes exhibited hierarchical habitat selection where snakes selected suitable microhabitats within preferred macrohabitats. To better examine habitat selection processes in the context of habitat disturbance, future studies need to include an adequate number of individuals from all reproductive classes within each disturbance category. It is optimal if researchers can monitor the same individuals prior to, during, and after disturbance similar to that demonstrated in Reinert et al. (2011) and MacGowan et al. (2017).

5. Conclusions

Overall, we found that radiotelemetry provides an effective method to evaluate the impacts of landscape disturbances on mobile and secretive vertebrates. Our study revealed that male *A. contortrix* used microhabitats with greater CWD cover and litter depth and less litter cover, pine tree species basal area, and canopy cover. Gravid females used microhabitats that possessed similar features as those used by male snakes (i.e., sites with deeper litter and greater CWD cover). At the macrohabitat scale, male snakes selected field and road edges and Southern Pine Beetle macrohabitats greater than their availability, whereas gravid female snakes did not demonstrate clear use patterns at the macrohabitat scales. Anecdotally, we noted that gravid female snakes tended to use open-canopy sites (either in Thinned Forest macrohabitats or sites with gaps from storm damage) during parturition. We found that thinning does not appear to impact home-range size of male *A. contortrix*; however, the macrohabitat analysis illustrated that Thinned Forest was not used greater than its availability by male snakes and that recently Thinned Forests possess different microhabitat and microclimate features of other used macrohabitats. Our study illustrates that both male and female *A. contortrix* used microhabitat sites with greater litter and CWD cover. In addition, male snakes in thinned stands used microhabitats that possessed lower air and soil temperature compared to random microhabitat sites. Collectively, used microhabitat sites likely provide prey ambush sites for male snakes and protection from potential predators along with quick access to varied thermal sites for both male and gravid female snakes. It is likely that other medium-large snake species require similar habitat features in disturbed landscapes. As our study was limited by our inability to monitor snakes prior to and after forest management across treatments, future research using telemetered individuals as indicators of forest management impacts should make efforts to design studies that incorporate spatial ecology and habitat use data prior to, during, and after forest management. If conservation of snakes and other forest-dwelling vertebrates is a management objective, maintenance of coarse-woody debris (i.e., cover objects >10 cm diameter), stumps and stumpholes, along with habitats within managed stands that possess deeper areas of litter cover will provide refuge habitats for a variety of these organisms until a harvested stand begins the process of ecological succession. Forest stands that succeed without additional forest management will increase in stem density for the first two decades after disturbance and will possess greater litter depth throughout this period. In addition, CWD will begin to accumulate along the forest floor, which will provide increased refuge and foraging sites. The periodic creation of canopy gaps (via natural or artificial means) is likely to provide thermoregulation, gestation, and foraging sites for *A. contortrix* after the forest canopy starts to close and become more homogeneous during later succession. Collectively, these habitat attributes are likely to encourage habitat use of *A. contortrix* for the next few decades following disturbance.

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References

Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74, 1313–1325.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67, 1–48.

Beyer, H.L., 2004. Hawth's Analysis Tools for ArcGIS Available at http://www.spatialecology.com/htools. Last accessed <8/20/2015>.

Blouin-Demers, G., Weatherhead, P.J., 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented habitats. Ecology 82, 2882–2896.

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., et al., 2013. The conservation status of the word's reptiles. Biol. Conserv. 157, 372–385.

Burbrink, F.T., Guiher, T.J., 2015. Considering gene flow when using coalescent methods to delimit lineages of North American pitvipers of the genus *Agkistrodon*. Zool. J. Linn. Soc.-Lon. 173, 505–526.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach. Springer Press, New York. 488 pp.

Bushar, L.M., Reinert, H.K., Gelbert, L., 1998. Genetic variation and gene flow within and between local populations of the timber rattlesnake, *Crotalus horridus*. Copeia 1998, 411–422.

Carfagno, G.L.F., Weatherhead, P.J., 2006. Intraspecific and interspecific variation in use of forest-edge habitat by snakes. Can. J. Zool. 84, 1440–1452.

Carfagno, G.L.F., Heske, E.J., Weatherhead, P.J., 2006. Does mammalian prey abundance explain forest-edge use by snakes? Ecoscience 13, 293–297.

Carpenter, J., 2009. Animal Space Use for ArcGIS v.1. Georgia Coastal Ecosystems LTER File Archive, University of Georgia, Athens, Georgia. (https://gce-lter.marsci.uga.edu/public/app/resource_details.asp?id=355). Last accessed <8/20/2015>.

Cincotta, R.P., Wisnewski, J., Engleman, R., 2000. Human population in the biodiversity hotspots. Nature 404, 990–992.

Compton, B.W., Rhymer, J.M., McCollough, M., 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83, 833–843.

Crane, A.L., Greene, B.D., 2008. The effect of reproductive condition on thermoregulation in female *Agkistrodon piscivorus* near the northwestern range limit. Herpetologica 64, 156–167.

Cross, C.L., Peterson, C.E., 2001. Modeling snake microhabitat from radiotelemetry studies using polytomous logistic regression. J. Herpetol. 35, 590–597.

Cross, M.D., Root, K.V., Mehne, C.J., McGowan-Stinski, J., Pearsall, D., Gillingham, J.C., 2015. Multi-scale responses of eastern massasauga rattlesnakes (*Sistrurus catenatus*) to prescribed fire. Am. Midl. Nat. 173, 346–362.

Degregorio, B.A., Manning, J.V., Bieser, N., Kingsbury, B.A., 2011. The spatial ecology of the eastern massasauga (*Sistrurus c. catenatus*) in northern Michigan. Herpetologica 67, 71–79.

DellaSala, D.A., Martin, A., Spivak, R., Schulke, T., Bird, B., Criley, M., van Daalen, C., et al., 2003. A citizen's call for ecological forest restoration: forest restoration principles and criteria. Ecol. Restoration 21, 14–21.

deMaynadier, P.G., Hunter Jr., M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environ. Rev. 3, 230–261.

Duncan, R.S., Linhoss, J.E., 2005. Regeneration of Virginia pine (*Pinus virginiana*) following southern pine beetle (*Dendroctonus frontalis*) outbreak in the Sipsey Wilderness, Alabama. Forest Ecol. Manage. 212, 65–74.

Durbian, F.E., 2006. Effects of mowing and summer burning on the massasauga (*Sistrurus catenatus*). Am. Midl. Nat. 155, 329–334.

Durbian, F.E., King, R.S., Crabill, T., Lambert-Doherty, H., Seigel, R.A., 2008. Massasauga home range patterns in the Midwest. J. Wildlife Manage. 72, 754–759.

Enge, K.M., 2001. The pitfalls of pitfall traps. J. Herpetol. 35, 467–478.

Fitch, H.S., 1960. Autecology of the copperhead. University of Kansas Publications Museum of Natural History 13, 85–288.

Fitch, H.S., Shirer, H.W., 1971. A radiotelemetric study of spatial relationships in some common snakes. Copeia 1971, 118–128.

Foster, M.S., Bissell, K.M., Campa III, H., Harrison, T.M., 2009. The influence of reproductive status on thermal ecology and vegetation use of female eastern Massasauga rattlesnakes (*Sistrurus catenatus catenatus*) in southwestern Michigan. Herp. Cons. Biol. 4, 48–54.

Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., et al., 2011. Completion of the 2006 national land cover database for the conterminous United States. Photogramm. Eng. Rem. S. 77, 858–864.

Garber, S., Burger, J., 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. Ecol. Appl. 5, 1151–1162.

Gaines, G.D., Creed, J.W., 2003. Forest health and restoration project. National forests in Alabama, Bankhead National Forest Franklin, Lawrence, and Winston Counties, Alabama. Final environmental impact statement. Manage. Bull. R8–MB 110B.

Germaine, S.S., Wakeling, B.F., 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. Biol. Conserv. 97, 229–237.

Gram, W.K., Sork, V.L., Marquis, R.J., Renken, R.B., Clawson, R.L., Faaborg, J., Fantz, D.K., Corff, J.L., Lill, J., Porneluzi, P.A., 2001. Evaluating the effects of ecosystem management: a case study in a Missouri Ozark forest. Ecol. Appl. 11, 1667–1669.

Greenberg, C.H., Neary, D.G., Harris, L.D., 1994. Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. Conserv. Biol. 8, 1047–1057.

Greenberg, C.H., Waldrop, T.A., 2008. Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest. Forest Ecol. Manage. 255, 2883–2893.

Harvey, D.S., Weatherhead, P.J., 2006. A test of the hierarchical model of habitat selection using eastern massasauga rattlesnakes (*Sistrurus c. catenatus*). Biol. Conserv. 130, 206–216.

Hassinger, J.S., 1989. Dead wood for wildlife. In: Finley, J.C., Brittingham, M.C. (Eds.), Timber Management and its Effects on Wildlife. Pennsylvania State University, University Park, Pennsylvania, pp. 171–184.

Howey, C.A.F., Dickinson, M.B., Roosenburg, W.M., 2016. Effects of a landscape disturbance on the habitat use and behavior of the black racer. Copeia 104, 853–863.

Horne, J.S., Garton, E.O., 2006. Selecting the best home range model: an information-theoretic approach. Ecology 87, 1146–1152.

Hoss, S.K., Guyer, C., Smith, L.L., Schuett, G.W., 2010. Multiscale influences of landscape composition and configuration on the spatial ecology of Eastern Diamondback Rattlesnakes (*Crotalus adamanteus*). J. Herpetol. 44, 110–123.

Johnson, G., 2000. Spatial ecology of the eastern massasauga (*Sistrurus c. catenatus*) in a New York peatland. J. Herpetol. 34, 186–192.

Kjoss, V.A., Litvaitis, J.A., 2001. Community structure of snakes in a human-dominated landscape. Biol. Conserv. 98, 285–292.

Knebel, L., Wentworth, T.R., 2007. Influence of fire and southern pine beetle on pine-dominated forests in the Linville Gorge Wilderness, North Carolina. Castanea 72, 214–225.

Loeb, S.C., 1999. Responses of small mammals to coarse woody debris. J. Mammal. 80, 460–471.

Lunney, D., Eby, P., O'Connell, M., 1991. Effects of logging, fire and drought on three species of lizards in Mumbulla state forest on the south coast of New South Wales Australia. Aust. J. Ecol. 16, 33–46.

Lutterschmidt, W.I., Reinert, H.K., 1990. The effect of ingested transmitters upon the temperature preference of the northern water snake, *Nerodia s. sipedon*. Herpetologica 46, 39–42.

MacGowan, B.J., Currylow, A.F.T., MacNeil, J.E., 2017. Short-term responses of Timber Rattlesnakes (*Crotalus horridus*) to even-aged timber harvests in Indiana. Forest Ecol. Manage. 387, 30–36.

Marshall Jr., J.C., Manning, J.V., Kingsbury, B.A., 2006. Movement and macrohabitat selection of the eastern massasauga in a fen habitat. Herpetologica 62, 141–150.

Mayor, S.J., Schneider, D.C., Schaefer, J.A., Mahoney, S.P., 2009. Habitat selection at multiple scales. Ecoscience 16, 238–247.

McKay, T.S., Komoroski, M.J., 2004. Demographic responses of shrews to removal of coarse woody debris in a managed pine forest. Forest Ecol. Manage. 189, 387–395.

Moore, J.A., Gillingham, J.C., 2006. Spatial ecology and multi-scale habitat selection by a threatened rattlesnake: the eastern Massasauga (*Sistrurus catenatus catenatus*). Copeia 2006, 742–751.

Myers, M., 1996. Environmental services of biodiversity. Proc. Natl. Acad. Sci. USA 93, 2764–2769.

Orians, G.H., Wittenberger, J.F., 1991. Spatial and temporal scales in habitat selection. Am. Nat. 137, S29–S49.

Pike, D.A., Webb, J.K., Shine, R., 2011. Removing forest canopy restores a reptile assemblage. Ecol. Appl. 21, 274–280.

Provencher, L., Litt, A.R., Gordon, D.R., 2003. Predictors of species richness in northwest Florida longleaf pine sandhills. Conserv. Biol. 17, 1660–1671.

R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reinert, H.K., Cundall, D., 1982. An improved surgical implantation method for radio-tracking snakes. Copeia 1982, 702–705.

Reinert, H.K., Kodrich, W.R., 1982. Movements and habitat utilization by the massasauga, *Sistrurus catenatus catenatus*. J. Herpetol. 16, 162–171.

Reinert, H.K., 1984a. Habitat separation between sympatric snake populations. Ecology 65, 478–486.

Reinert, H.K., 1984b. Habitat variation within sympatric snake populations. Ecology 65, 1673–1682.

Reinert, H.K., Cundall, D., Bushar, L.M., 1984. Foraging behavior of the timber rattlesnake, *Crotalus horridus*. Copeia 1984, 976–981.

Reinert, H.K., 1993. Habitat selection in snakes. In: Seigel, R.A., Collins, J.T. (Eds.), Snakes: Ecology and Behavior. McGraw-Hill Publishing Company, New York, pp. 201–240.

Reinert, H.K., Munroe, W.F., Brennan, C.E., Rach, M.N., Pelesky, S., Bushar, L.M., 2011. Response of timber rattlesnakes to commercial logging operations. J. Wildlife Manage. 75, 19–29.

Richardson, M.L., Weatherhead, P.J., Brawn, J.D., 2006. Habitat use and activity of prairie kingsnakes (*Lampropeltis calligaster calligaster*) in Illinois. J. Herpetol. 40, 423–428.

Row, J.R., Blouin-Demers, G., 2006. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. Ecoscience 13, 443–450.

Russell, K.R., Wigley, T.B., Baughman, W.M., Hanlin, H.G., Ford, W.M., 2004. Responses of southeastern amphibians and reptiles to forest management: a review. In: Rauscher, M.H., Johnsen, K., (Eds.), Southern Forest Science: Past, Present, and Future. United States Department of Agriculture Southern Research Station Gen. Tech. Rep. SRS–75, pp. 319–334.

Ryan, T.J., Philippi, T., Leiden, Y.A., Dorcas, M.E., Wigley, T.B., Gibbons, J.W., 2002. Monitoring herpetofauna in a managed forest landscape: effects of habitat types and census techniques. Forest Ecol. Manage. 167, 83–90.

Schweitzer, C.J., Tadesse, W., 2004. The interaction of fire frequency and stand density on plant community dynamics. In: CREST–Center for Forest Ecosystem Assessment (CFEA) Alabama A&M University. National Science Foundation proposal, pp. 1–14.

Seigel, R.A., Pilgrim, M.A., 2002. Long-term changes in movement patterns of massasaugas (*Sistrurus catenatus*). In: Schuett, G.W., Hoggren, M., Douglas, M.E., Greene, H.W. (Eds.), Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, Utah, USA, pp. 405–412.

Semlitsch, R.D., Todd, B.D., Blomquist, S.M., Calhoun, A.J.K., Gibbons, J.W., Gibbs, J.P., et al., 2009. Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. BioScience 59, 853–862.

Smalley, G.W., 1982. Classification and evaluation of forest sites on the mid-Cumberland Plateau. U.S. Department of Agriculture Forest Service, General Technical Report S0–38. Southern Forest Experimental Station, New Orleans, Louisiana, 58 pp.

Smith, C.F., Schuett, G.W., Earley, R.L., Schwenk, K., 2009. The spatial and reproductive ecology of the copperhead (*Agkistrodon contortrix)* at the northeastern extreme of its range. Herpetol. Monogr. 23, 45–73.

Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P.K.L., 2004. Southeast Asian biodiversity: an impending disaster. Trends Ecol. Evol. 19, 654–660.

Sperry, J.H., Weatherhead, P.J., 2009. Does prey availability determine seasonal patterns of habitat selection in Texas ratsnakes? J. Herpetol. 43, 55–64.

Sperry, J.H., Weatherhead, P.J., 2010. Ratsnakes and brush piles: intended and unintended consequences of improving habitat for wildlife? Am. Midl. Nat. 163, 311–317.

SPSS Inc., Released 2016. PASW Statistics for Windows, Version 24.0. Chicago: SPSS Inc.

Steen, D.A., 2010. Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. Herp. Cons. Biol. 5, 183–188.

Steen, D.A., McClure, C.J.W., Brock, J.C., Rudolph, D.C., Pierce, J.B., Lee, J.R., et al., 2012. Landscape-level influences of terrestrial snake occupancy with the southeastern United States. Ecol. Apps. 22, 1084–1097.

Steen, D.A., McClure, C.J.W., Sutton, W.B., Rudolph, D.C., Pierce, J.B., Lee, J.R., et al., 2014. Copperheads are common when kingsnakes are not: relationships between the abundances of a predator and one of their prey. Herpetologica 70, 69–76.

Sutton, W.B., Wang, Y., Schweitzer, C.J., 2010. Habitat relationships of reptiles in pine beetle disturbed forests of Alabama, U.S.A. with guidelines for a modified drift-fence sampling method. Curr. Zool. 56, 411–420.

Sutton, W.B., Wang, Y., Schweitzer, C.J., 2013. Amphibian and reptile responses to thinning and prescribed burning in mixed pine-hardwood forest of northwestern Alabama, USA. Forest Ecol. Manage. 295, 213–227.

Sutton, W.B., Wang, Y., Schweitzer, C.J., Steen, D.A., 2014. Lizard microhabitat and microclimate relationships in southeastern pine-hardwood forests managed with prescribed burning and thinning. Forest Sci. 60, 180–190.

Thompson III, F.R., Dijak, W., Burhans, D.E., 1999. Video identification of predators at songbird nests in old fields. Auk 116, 259–264.

Tilghman, J.M., Ramee, S.W., Marsh, D.M., 2012. Meta-analysis of the effects of canopy removal on terrestrial salamander populations in North America. Biol. Conserv. 152, 1–9.

Todd, B.D., Andrews, K.M., 2007. Response of a reptile guild to forest harvesting. Conserv. Biol. 22, 753–761.

Vitt, L.J., Avila-Pires, T.C.S., Caldwell, J.P., Oliveira, V.R.L., 1998. The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. Conserv. Biol. 12, 654–664.

Waldron, J.L., Bennett, S.H., Welch, S.M., Dorcas, M.E., Lanham, J.D., Kalinowsky, W., 2006. Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. Animal Conserv. 9, 414–420.

Waldron, J.L., Welch, S.M., Bennett, S.H., 2008. Vegetation structure and the habitat specificity of a declining North American reptile: a remnant of former landscapes. Biol. Conserv. 141, 2477–2482.

Weatherhead, P.J., Blouin-Demers, G., 2004. Understanding avian nest predation: why ornithologists should study snakes. J. Avian Biol. 35, 185–190.

Weatherhead, P.J., Carfagno, G.L., Sperry, J.H., Brawn, J.D., Robinson, S.K., 2010. Linking snake behavior to nest predation in a Midwestern bird community. Ecol. Appl. 20, 234–241.

Webb, J.K., Shine, R., Pringle, R.M., 2005. Canopy removal restores habitat quality for an endangered snake in a fire suppressed landscape. Copeia 2005, 895–900.

Wiens, J.A., Rotenberry, J.T., Horne, B.V., 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effect of spatial scale. Oikos 48, 132–147.