Habitat selection and movement patterns of copperheads (*Agkistrodon contortrix*) in fire-altered landscapes

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By

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James P. Flaherty   June 21, 2016

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DEDICATION

I dedicate this work to my friend of 10 years, Wookie. Hope you're eating scrambled

eggs and strawberries in lizard heaven, buddy.

ACKNOWLEDGMENTS

ABSTRACT

Habitat selection and movement patterns of copperheads (*Agkistrodon contortrix*) in fire-altered landscapes

Fire can functionally alter habitat available to wildlife through modification of structural and micro-climatic characteristics. Because of their reliance on behavioral thermoregulation and crypsis, reptiles can be especially susceptible to these post-fire changes in habitat characteristics. The copperhead (*Agkistrodon contortrix*) is a widely distributed snake found throughout the southeastern US, and is found in a variety of habitats. Previous studies suggest that copperheads decrease in abundance after fire events, and in order to investigate the specific drivers influencing these changes in abundance, we radio-tracked 14 adult male copperheads captured in burned and unburned habitats at Land Between the Lakes National Recreation Area, KY. Copperheads were tracked during the active season (May-October) of 2014 and 2015. Home ranges were calculated by minimum convex polygons (MCP) and fixed kernel density estimation (KDE). Movement patterns were assessed by estimating the distance moved per day. At each copperhead relocation, a suite of structural and environmental habitat variables were recorded and each relocation point was paired with a randomly selected point to assess habitat availability. Copperheads in burned areas were more likely to use shrub thickets as cover, while those in unburned areas were more likely to use leaf and woody debris piles. There was no significant difference between estimated distance moved per day of copperheads in burned and unburned areas but MCP and KDE home ranges of copperheads in unburned areas were significantly larger than those in burned areas. Because of increased habitat heterogeneity after fire, we suggest that fire-altered

landscapes may be more suitable habitat for copperheads than landscapes lacking

disturbance.

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Chapter I

Introduction

Disturbances are a natural part of ecosystem succession and functionality (White 1979, Sousa 1984). Landscapes subjected to periodic disturbances often contain a patchy mosaic of varying habitat structure and environmental conditions (Baker 1992). These heterogeneous landscapes typically have the capacity to support a wider diversity of species than homogeneous landscapes due to the greater variability in available resources, resulting in greater niche diversity (Bazzaz 1975, Tews et al. 2004). Tests of the intermediate disturbance hypothesis support this contention, and ecological communities that exhibit moderate amounts of disturbance tend to be the most speciose (Connell 1978, Roxburgh et al. 2004). For some species, a predictable or recurring regime of disturbance is likely necessary for long-term persistence. This is especially true of species assemblages in disturbance-prone landscapes, such as floodplains (Ward 1998), grasslands (Belsky 1992), and fire-adapted systems (Hawkes and Menges 1996, Simon et al. 2009). More generalist species may persist, or even thrive, in areas where the natural disturbance regime is altered or eliminated. This can potentially be explained by the wide niche breadth often attributed to generalist species, allowing for persistence in a diversity of habitat types and, in some cases, permitting a large geographic range (Slatyer et al. 2013).

Fire is a naturally occurring form of disturbance, which can alter structural and environmental conditions depending on frequency and intensity. Low-intensity fires of moderate frequency can modify the landscape through reduction of leaf litter, woody debris, and woody stem regeneration, as well as promotion of understory herbaceous

plant communities (Hutchinson *et al.* 2005). High-intensity fires can often be catastrophic, resulting in die-offs of entire stands of trees and radically reducing canopy closure (Vose *et al.* 1999), whereas low frequency fires can increase the growth of dense thickets of woody stems (Peterson and Reich 2001). Increased exposure to solar radiation as well as reduction in surface structure (i.e. leaf litter and woody debris) can also result in increased soil temperature and reduced soil moisture in fire-altered areas (Iverson and Hutchinson 2002).

The wildlife response to fire-altered landscapes has been relatively well-studied in a diverse array of taxa, including invertebrates (Wikars and Schimmel 2001), amphibians (Pilliod *et al.* 2003, O'Donnell *et al.* 2015), birds (Bock and Block 2005, Saab and Powell 2005), and small mammals (Ford *et al.* 1999, Eby *et al.* 2014). Reptiles have also been well studied, with the majority of previous work focused on changes in species abundance and diversity in post-fire landscapes (Mushinsky 1985, Perry *et al.* 2009, Sutton *et al.* 2013). It is likely that many of these changes in abundance and diversity are driven by the alteration of species-specific traits in response to fire. In the cases of pygmy bluetongue lizards (*Tiliqua adelaidensis*) in South Australia (Fenner and Bull 2007) and Orsini's vipers (*Vipera ursinii*) in the French Alps (Lyet *et al.* 2009), a reduction in body condition immediately after fire is directly attributed to measured changes in prey availability and greater visibility to potential predators. Smith *et al.* (2001) observed a decrease in movement and an increase in use of underground refugia in three species of montane rattlesnakes after fire altered the landscape. Developing a better understanding of how fire-related disturbances influence the behavior of resident species may shed light onto the specific drivers of changes in reptile community composition.

Historically, much of the southeastern United States underwent a periodic cycle of fires ignited by lightning strikes (Abrams 1992, Waldrop *et al.* 1992, Frost 1998). There is also evidence of fire being used consistently as a land management tool by pre-Columbian Native Americans throughout much of the southeast (Delcourt and Delcourt 1997). The historic cycle of fire-related disturbance was extensively altered in the region after European settlement, with widespread fire suppression eventually adopted as the dominant land management strategy (Pyne 1982, Stephens and Ruth 2005). Only recently have land managers in the southeastern United States begun using controlled fire, referred to as prescribed fire, as a technique to replicate historic fire frequencies and increase local species diversity (Pyne *et al.* 1996). The application of prescribed fire to the landscape allows for the opportunity to investigate how certain species respond to fire as a form of disturbance.

The copperhead (*Agkistrodon contortrix*) is a geographically widespread species of viperid snake, and is considered a generalist where it occurs in the southeastern United States (Ernst and Ernst 2003). The ability to persist in both fire-maintained and fire-suppressed forest habitats make copperheads an ideal species to investigate behavioral responses to fire. Previous research suggests that copperheads are either less abundant in areas impacted by prescribed fire (Howey 2014) or remain largely unaffected (Perry *et al.* 2009, Sutton *et al.* 2013). To investigate the behavioral response of copperheads to fire-associated habitat alteration, habitat selection and movements in fire-altered and fire-suppressed landscapes were compared. Based on the previous findings suggesting a positive relationship with unburned habitat, it was predicted that copperheads would select habitats most similar to those available in fire-suppressed areas and that

movements would be greater in distance and frequency in potentially less preferred fire-altered areas.

Chapter II

Methods

Study site

All aspects of this study were conducted at Land Between the Lakes National Recreation Area (LBL) in Trigg County, Kentucky. LBL is at the edge of the western Highland Rim of the Interior Low Plateaus physiographic region (Fenneman 1938), which typically exhibits hilly terrain with steep dry slopes. The majority of LBL is forested, with upland sites being dominated by secondary oak-hickory forest (Close *et al.* 2002), but historically much of LBL consisted of open oak-savanna maintained by grazing megafauna and periodic fire (Franklin *et al.* 2002). Active fire suppression, beginning in the 1950s, has lead to widespread succession towards more closed-canopied forest (Franklin *et al.* 1993). As a result, most of LBL has not been burned in 60-80 years (Franklin 1994). In order to improve recreation opportunities and restore historic oak-savanna habitat, prescribed fire has been recently adopted as a land management tool throughout LBL (USDA Forest Service 2004). In April 2007 and again in September 2010, an area of approximately 1,000 ha (Franklin Creek Burn Area; Figure 1) was burned using a helicopter to drop plastic incendiary spheres filled with potassium permanganate (Howey 2014). Although frontal fire intensity was not measured at the time of either burn, due to the controlled nature of prescribed fires and the generally low slope angle of the burn sites, both burns were likely of low intensity (Alexander 1982, Franklin *et al.* 2003).

Radio telemetry

Copperheads were initially located via haphazard survey of appropriate habitat and nocturnal road-cruising in the Franklin Creek Burn Area (Burn) and adjacent

unburned areas within three km of the Franklin Creek Burn Area (Control) from May 2014 through July 2015. At time of capture, snout-vent length (SVL) and tail length (TL) of each snake was measured to the nearest 1 mm, body mass was measured to the nearest 1 g, and sex was determined by cloacal probing. Snakes were uniquely marked by sub-dermal injection of a Passive Integrated Transponder (PIT tag, Biomark Inc., Boise, ID). Only male snakes were used in this study because of known intersexual differences in movements and thermal biology of temperate zone pit-vipers (Fitch 1960, Reinert and Zappalorti 1988, Shine *et al.* 2003). Copperheads were transported to a field laboratory (Hancock Biological Station), where they were surgically implanted with a radio transmitter (SI-2, Holohil Systems Ltd., Carp, ON, Canada) that weighed no more than 7% of body mass. Surgeries were conducted following the methods of Reinert and Cundall (1982) and snakes were allowed 24-48 hours to recover from surgery before release at the point of capture. Snakes were thereafter relocated every 2-5 days from mid May through early October (active season) between 9:00-18:00 hours. At each snake location, Universal Transverse Mercator (UTM) coordinates were recorded in NAD83 datum using a GPSmap 60CSx (Garmin International Inc., Olathe, KS). All locations were recorded to an accuracy of ≤ 3 meters. Sometimes snakes crossed over between habitat types and snakes were considered either Burn or Control when they spent at least 65% of time in one of the habitat types.

Microhabitat Analysis
During the 2014 field season a suite of 18 environmental and habitat structural variables were recorded at each snake location (Table 1). A 1-m^2 quadrat was established centered on the snake location. To measure the habitat available for use by copperheads, each snake relocation point was paired with a randomly selected point. Random points

were selected by walking a randomly selected straight-line distance (within 60 m) away from the snake point at a randomly chosen compass bearing. At this random point, the same suite of environmental and habitat structural variables were also measured (Table 1). Cover objects were defined as any physical object a copperhead could conceivably use to fully or partially seek refuge. Environmental and habitat structural variables for snake and random locations in burn and unburned areas were compared using repeated-measures ANOVA with individual snake and random point grouping as a repeated factor, followed by post-hoc Tukey's HSD comparison of means and control of false discovery rate (Benjamini and Hochberg 1995).

Movements and Home Range
Distance moved per day was calculated for each copperhead as the distance between relocations divided by the number of days elapsed between relocations. Distance moved per day within the burn area was compared to those captured outside the burn area using repeated-measures ANOVA with individual snake being the repeated factor. Movements of ≤ 3 m were excluded from analyses due to location accuracy. Home range size of radio-tracked copperheads was calculated using the 100% minimum convex polygon method (MCP; Burt 1943) as well as 95% and 50% fixed kernel density estimators (KDE; Worton 1989) using a least square cross validation smoothing parameter (Seaman and Powell 1996). Home range sizes of copperheads captured within the burn area were compared to those captured outside the burn area using a general linear model, with site (Burn or Control) as the main effect, individual snake and year tracked as random effects, and duration of active season radio-tracking used as a covariate. Home range estimation and movement patterns were calculated using Geospatial Modeling Environment (Spatial Ecology LLC, Toronto, Canada) and ArcGIS

10.2.2 (ESRI, Redlands, CA). All statistical analyses were conducted using JMP version 10 (SAS Institute Inc., Cary, NC) and test were considered significant using $\alpha = 0.05$.

Chapter III

Results

A total of five copperheads were captured in burn areas (Burn Snakes) and nine from unburned areas (Control Snakes). Five copperheads (2 Burn Snakes and 3 Control Snakes) were radio-tracked during both the 2014 and 2015 field seasons due to losses from overwintering mortality and additions resulting from new 2015 captures.

Microhabitat Analysis

Of the 18 environmental and habitat structural variables recorded, five variables were significantly different among the four sampling groups (Table 2). Burn Random locations exhibited significantly higher surface temperature than Control Snake locations (FDR adjusted $P = 0.04$; Figure 2). Control Snake locations exhibited greater surface woody debris cover that Control Random locations (FDR adjusted $P = 0.01$; Figure 3). Control Snake locations exhibited deeper leaf litter than Control Random locations (FDR adjusted $P = 0.04$; Figure 4). Burn Snake locations exhibited greater woody stem density than both Burn Random locations and Control Random locations (FDR adjusted $P = 0.009$; Figure 5). Burn Snake locations were closer to cover than Control Random locations, while Control Snake locations were closer to cover than both Burn and Control Random locations (FDR adjusted $P = 0.002$; Figure 6).

Home Range and Movements

All copperheads included in the analysis of movement and home range were radio-tracked for a minimum of 64 days during the spring and summer seasons. No significant difference between Burn Snakes and Control Snakes was found when comparing approximate distances moved per day ($R^2 = 0.26$, $F_{1,17} = 0.03$, $P = 0.87$). Home range sizes varied by individual, and overall KDE home range sizes were larger

than those measured via MCP (Table 3). Duration of active season radio-tracking was found to have a significant effect on home range size (MCP $P = 0.002$, 95% KDE $P = 0.0006$, 50% KDE $P = 0.0001$), while year tracked did not (MCP $P = 0.64$, 95% KDE $P = 0.62$, 50% KDE $P = 0.56$; Table 4). After controlling for the significant effect of tracking duration (model covariate), home ranges of Control Snakes were found to be significantly larger than those of Burn Snakes for all home range estimators (MCP $R^2 = 0.66$, $F_{1,17} = 5.69$, $P = 0.04$; 95% KDE $R^2 = 0.60$, $F_{1,17} = 11.9$, $P = 0.008$; 50% KDE $R^2 = 0.70$, $F_{1,17} = 19.5$, $P = 0.003$; Table 4).

Chapter IV

Discussion

The results of this study suggest that landscape alterations resulting from prescribed fire management change the manner in which copperheads interact with their environment. Even with a small sample size and short study duration, significant differences were observed in terms of home range size and habitat selection between copperheads in burned and unburned areas.

Microhabitat Analysis

Point measurements of temperature were collected to compare the thermal environment of burned and unburned areas. Ambient and soil temperatures did not differ among the sampling locations, but measured differences in surface temperature suggest that copperheads are selecting cooler locations within the landscape and that the forest floor of burned areas is warmer than that of unburned areas. A more complete representation of the thermal environment would likely require constant temperature measurement.

Copperheads in both burned and unburned areas were almost always found in close proximity to some type of cover. Throughout much of their active season, copperheads are primarily nocturnal (Ernst and Ernst 2003) and likely select sufficient cover in order to retreat during the daylight hours. Previous studies have shown that some species of nocturnal snakes will actively select diurnal retreat sites based on specific criteria regarding the temperature and structure of cover (Webb *et al.* 2004). Our results suggest that copperheads in unburned areas are selecting locations with more woody debris and deeper leaf litter, while copperheads in burned areas are selecting locations of dense woody stems. This observed variation in cover selection might be representative of

a differing availability of diurnal retreat sites in burned and unburned areas. Although anecdotal in nature, our field observations during this study support this assumption, with copperheads in unburned areas often seen associated with piles of leaves and woody debris adjacent to downed trees and canopy gaps, while copperheads in burned areas lacking leaf litter and debris were often seen associated with dense thickets of early successional shrubs, such as blackberry (*Rubus sp.*) and poison ivy (*Toxicodendron radicans*).

Movements and Home Range
No observable difference was noted between copperhead movements in burned and unburned areas using estimated distance moved per day as a metric of fine scale spatial habitat use. Although this method has been extensively used in movement studies of snakes (Fitch and Shirer 1971, Reinert and Kodrich 1982, Gerald *et al.* 2012), the use of linear distances based on fixed-point data may not be the best approximation of snake movement rates because they do not take into account the potential tortuosity of the animal's movement. Secor (1994) compared linear measurement of movements based on fixed-point data to true extent of movement based on tracks left in the sand of sidewinders (*Crotalus cerastes*) and found that linear measurements underestimated the full extent of movement by up to 60 percent. Based on data collected during telemetry studies of four ecologically distinct species of African snakes (*Bitis arientans, B. schneideri, Python natalensis*, and *Gonionotophis capensis*), Alexander and Maritz (2015) argue that measurements of movement distances based on fixed-point data are strongly impacted by variations in sampling frequency. It is possible that the sampling interval used in this study (2-5 days) influenced measurements of daily linear distances to a point where they were no longer accurate representations of snake movement.

Many factors have the capacity to influence the space use of an animal. In snakes, intrinsic factors, such as body size and sex (Smith *et al.* 2009, Glaudas and Rodriguez-Robles 2011, Hyslop *et al.* 2014), have well-documented influences on intraspecific variations in home range size. Extrinsic factors, such as habitat suitability, also have the potential to influence the amount of area used. In comparatively resource-poor landscapes, animals may need to use larger geographic areas to acquire enough resources to execute basic life functions. Kapfer *et al.* (2010) found that bullsnakes (*Pituophis cantifer*) in landscapes containing high proportions of less suitable habitat (agricultural fields and closed-canopy forests) have significantly larger home ranges than those in landscapes containing higher proportions of more suitable habitat (bluff faces and oak savanna). Similarly, Halstead *et al.* (2009) found that coachwhips (*Coluber flagellum*) utilizing greater proportions of the study population's preferred habitat type (Florida scrub) exhibited significantly smaller home range sizes. When applying this assumption of smaller home range size implying greater habitat suitability to our study, it can be suggested that since copperheads in the burn areas exhibited smaller home ranges, burn areas may be more suitable habitat for copperheads than unburned areas. Potential factors influencing the degree of habitat suitability exhibited by a particular landscape can be difficult to quantify. Prey density, predation pressure, thermoregulatory opportunities, and refuge availability have all been suggested as potential factors mediating movement behaviors based on habitat suitability in snakes (Baxley and Qualls 2009, Halstead *et al.* 2009, Hoss *et al.* 2010, Kapfer *et al.* 2010). Preliminary findings from a study conducted at this same site suggest that during most of the spring and summer copperheads do not display overt thermoregulatory behaviors (Mueller, unpublished data), and are therefore

likely not basing movement behaviors around assessing thermoregulatory opportunities at that particular time of the year. In our study, refuge availability was quantified by measuring cover type and density. Due to their strong reliance on crypsis (Ernst and Ernst 2003), refuge availability is likely a major factor when characterizing copperhead habitat suitability. By frequently using shrubby thickets as cover, copperheads in burned areas may not need to travel very far to find appropriate diurnal retreat locations. With unburned areas having reduced mid and understory vegetation, copperheads in those areas may be forced to travel farther to find cover in the form of leaf and woody debris piles.

It is also likely that refuge type and availability are not the only factors influencing copperhead movements at these locations. Although a dietary generalist, in this region previous studies have found that the majority of copperhead diet is composed of rodents (Garton and Dimmick 1969). The population dynamics of many rodents are primarily driven by oak mast production and availability (Ostfeld et al. 1996, Wolf 1996, Feldhamer et al. 2002). The presence of fire disturbance has been found to promote oak regeneration by arresting succession towards mesic maple-dominated forests (Abrams 1992, Franklin et al. 2002). Because of this, it is possible that the burned areas in LBL contain a greater proportion of acorn-bearing oaks, and therefore would support greater densities of mammalian prey species. It must also be taken into account that although all copperheads in this study were male, their movements were likely strongly influenced by the abundance and distribution of female copperheads within their area of activity (Smith et al. 2009).

Conclusion

It was initially predicted that, based on previous studies of abundance, copperheads would likely prefer areas unaltered by fire disturbance. However, our results suggest that fire-altered landscapes are likely more suitable habitat for copperheads. Although seemingly contradictory, it is possible that both arguments are valid. Previous studies of post-fire copperhead abundance in which we based our prediction were conducted one to two years after prescribed burning was implemented (Perry *et al* 2009, Howey 2014). These early successional landscapes were sampled immediately after the burn and may have initially been poor habitat for copperheads. Our study of copperhead movements and habitat selection was conducted four to five years after prescribed burning was implemented. The greater amount of time since the landscape was burned has allowed much of the burned areas to progress into a mid-successional landscape with dense thickets of shrubs, providing abundant cover for copperheads. The persistence of such differences, even after habitats have begun to recover, indicates the long-lasting effects habitat alterations may have on the ecology of even generalist species, like copperheads. When considering both our results as well as those of previous studies, it is likely that the frequency of landscape disturbance is equally as an important factor as the absence of disturbance when characterizing the preferred habitats of copperheads.

Chapter V

Tables and Figures
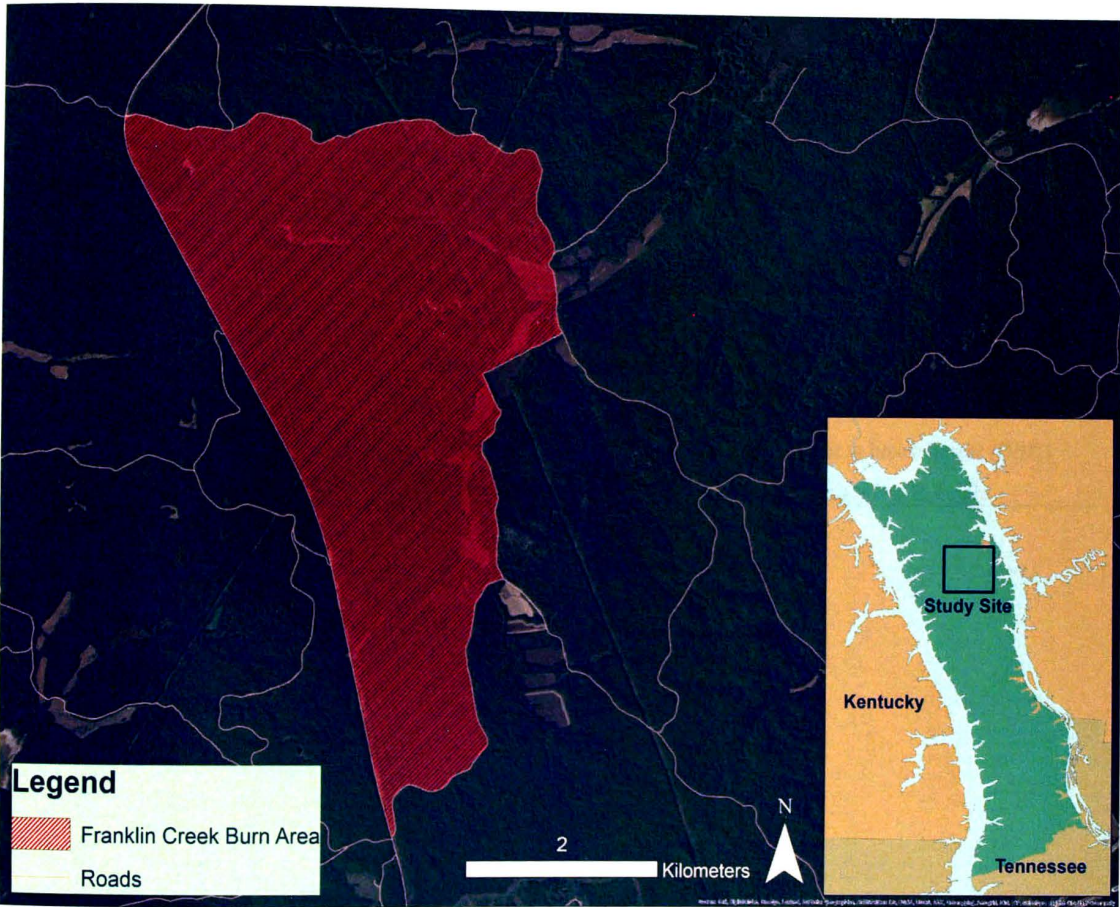
Figure 1. Map displaying the Franklin Creek Burn Area and adjacent unburned locations. Area in red was burned in April 2007 and September 2010 and adjacent wooded habitat had not been burned ≥ 60 years.

Table 1. Environmental and structural variables collected at each copperhead and random location.

Variable	Sampling method
Ambient Temperature	Temperature (°C) of air at 1 m above snake
Surface Temperature	Temperature (°C) of substrate surface within 10 cm of snake
Soil Temperature	Temperature (°C) of soil within 10 cm of snake
Canopy Closure	% canopy closure measured using a spherical densiometer
Surface Leaf Litter Cover	% leaf litter cover within 1-m^2 quadrat
Surface Woody Debris Cover	% woody debris cover within 1-m^2 quadrat
Surface Herbaceous Cover	% herb (non-woody plants) cover within 1-m^2 quadrat
Surface Grass Cover	% grass cover within 1-m^2 quadrat
Surface Bare Ground Cover	% bare ground cover within 1-m^2 quadrat
Surface Rock Cover	% rock cover within 1-m^2 quadrat
Leaf Litter Depth	Depth (cm) of leaf litter within 10 cm of snake
Woody Stem Density	Total number of woody stems within 1-m^2 quadrat
Woody Stem Height	Height (m) of tallest woody stem within 1-m^2 quadrat
Distance to Cover	Distance (m) to nearest cover object
Cover Height	Height (cm) of nearest cover object
Cover Length	Length (cm) of nearest cover object
Distance to Overstory Tree	Distance (m) to nearest tree ≥ 7.5 cm diameter at breast height (DBH)
Distance to Understory Tree	Distance (m) to nearest tree < 7.5 cm DBH and > 2 m in height

Table 2. Least square mean values and standard error (SE) of environmental and structural habitat variables measured at snake and random locations. Least square mean values having different superscript are significantly different based on repeated-measures ANOVA and post-hoc Tukey's HSD tests. P-values were adjusted to control for false discovery rate. Variables that differed significantly are in bold.

| Variable	Burn Snake (n = 79)		Control Snake (n = 138)		Burn Random (n = 75)		Control Random (n = 138)		ANOVA results	P	FDR adj P
	Mean	SE	Mean	SE	Mean	SE	Mean	SE			
Ambient Temperature (°C)	27.9^{A}	0.4	27.0^{A}	0.3	28.1^{A}	0.4	26.9^{A}	0.3	$F_{3,430} = 2.81$	0.07	0.14
Surface Temperature (°C)	$\mathbf{28.1^{AB}}$	**0.6**	$\mathbf{26.7^{B}}$	**0.4**	$\mathbf{29.5^{A}}$	**0.6**	$\mathbf{27.7^{AB}}$	**0.4**	$\mathbf{F_{3,430} = 4.87}$	**0.01**	**0.04**
Soil Temperature (°C)	18.4^{A}	0.3	17.4^{A}	0.2	18.4^{A}	0.3	17.8^{A}	0.2	$F_{3,430} = 3.28$	0.04	0.12
Canopy Closure (%)	81.9^{A}	4.2	84.2^{A}	3.4	75.6^{A}	4.2	80.1^{A}	3.4	$F_{3,430} = 0.88$	0.46	0.59
Surface Leaf Litter Cover (%)	42.2^{A}	5.6	52.2^{A}	4.8	44.3^{A}	5.7	55.1^{A}	4.7	$F_{3,430} = 2.73$	0.05	0.13
Surface Woody Debris Cover (%)	$\mathbf{18.4^{AB}}$	**2.9**	$\mathbf{24.9^{A}}$	**2.4**	$\mathbf{16.2^{AB}}$	**3.1**	$\mathbf{11.1^{B}}$	**2.4**	$\mathbf{F_{3,430} = 5.86}$	**0.002**	**0.01**
Surface Herbaceous Cover (%)	23.6^{A}	2.6	15.7^{B}	2.0	17.6^{AB}	2.7	15.7^{AB}	2.0	$F_{3,430} = 2.70$	0.06	0.14
Surface Grass Cover (%)	20.3^{A}	6.1	10.8^{A}	5.5	12.5^{A}	6.2	19.0^{A}	5.5	$F_{3,430} = 1.68$	0.18	0.27
Surface Open Ground Cover (%)	6.20^{A}	5.6	6.76^{A}	5.2	13.1^{A}	4.6	16.1^{A}	4.4	$F_{3,430} = 1.04$	0.38	0.53
Surface Rock Cover (%)	5.68^{A}	4.4	9.16^{A}	3.7	19.7^{A}	3.9	13.7^{A}	3.5	$F_{3,430} = 2.05$	0.12	0.69
Leaf Litter Depth (cm)	$\mathbf{7.14^{AB}}$	**1.0**	$\mathbf{9.71^{A}}$	**0.7**	$\mathbf{6.53^{AB}}$	**1.0**	$\mathbf{6.10^{B}}$	**0.7**	$\mathbf{F_{3,430} = 4.95}$	**0.008**	**0.04**
Woody Stem Density	$\mathbf{7.08^{A}}$	**0.5**	$\mathbf{5.10^{AB}}$	**0.4**	$\mathbf{4.80^{B}}$	**0.6**	$\mathbf{3.54^{B}}$	**0.4**	$\mathbf{F_{3,430} = 9.00}$	**0.001**	**0.009**
Woody Stem Height (m)	2.04^{A}	0.5	2.67^{A}	0.4	0.95^{A}	0.5	1.65^{A}	0.4	$F_{3,430} = 2.57$	0.09	0.16
Distance to Cover (m)	$\mathbf{0.72^{AB}}$	**0.2**	$\mathbf{0.60^{A}}$	**0.1**	$\mathbf{1.29^{BC}}$	**0.1**	$\mathbf{1.55^{C}}$	**0.1**	$\mathbf{F_{3,430} = 11.4}$	**< 0.0001**	**0.002**
Cover Height (cm)	23.9^{A}	4.0	26.5^{A}	3.1	23.0^{A}	4.0	21.1^{A}	3.1	$F_{3,430} = 0.52$	0.67	0.75
Cover Length (cm)	495^{A}	60	528^{A}	45	502^{A}	61	440^{A}	45	$F_{3,430} = 0.67$	0.58	0.69
Distance to Overstory Tree (m)	3.66^{A}	0.6	3.72^{A}	0.5	3.57^{A}	0.6	3.23^{A}	0.5	$F_{3,430} = 0.21$	0.89	0.94
Distance to Understory Tree (m)	1.59^{A}	0.4	1.44^{A}	0.4	1.64^{A}	0.4	1.74^{A}	0.4	$F_{3,430} = 0.13$	0.94	0.94
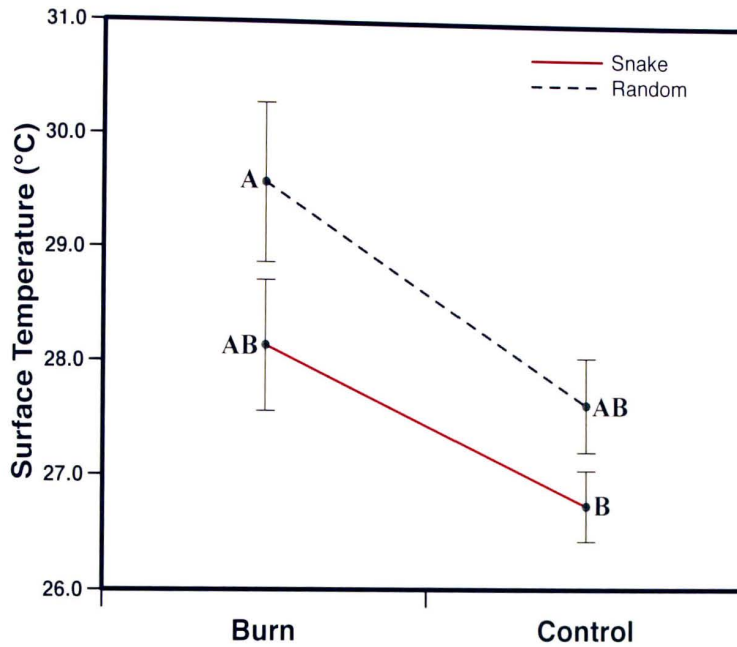
Figure 2. Interaction plots comparing the mean and standard error of surface temperature measured at snake and random locations. Mean values displaying different letters are significantly different based on repeated-measures ANOVA and post-hoc Tukey's HSD tests. Burn Random locations exhibited significantly higher surface temperature than Control Snake locations (FDR adjusted P = 0.04).

Figure 3. Interaction plots comparing mean and standard error of surface woody debris cover measured at snake and random locations. Mean values displaying different letters are significantly different based on repeated-measures ANOVA and post-hoc Tukey's HSD tests. Control Snake locations exhibited greater surface woody debris cover that Control Random locations (FDR adjusted P = 0.01).

Figure 4. Interaction plots comparing mean and standard error of leaf litter depth measured at snake and random locations. Mean values displaying different letters are significantly different based on repeated-measures ANOVA and post-hoc Tukey's HSD tests. Control Snake locations exhibited deeper leaf litter than Control Random locations (FDR adjusted $P = 0.04$).
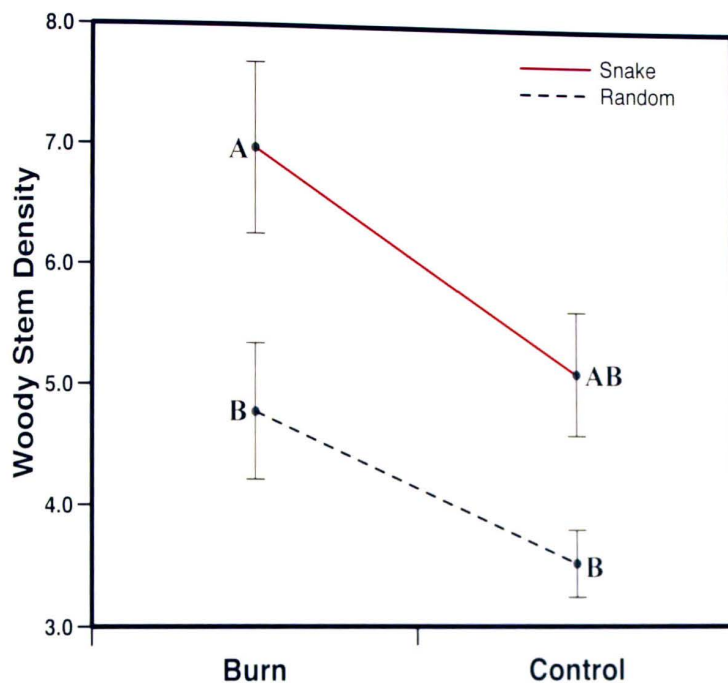
Figure 5. Interaction plots comparing mean and standard error of woody stem density measured at snake and random locations. Mean values displaying different letters are significantly different based on repeated-measures ANOVA and post-hoc Tukey's HSD tests. Burn Snake locations exhibited greater woody stem density than both Burn Random locations and Control Random locations (FDR adjusted P = 0.009).

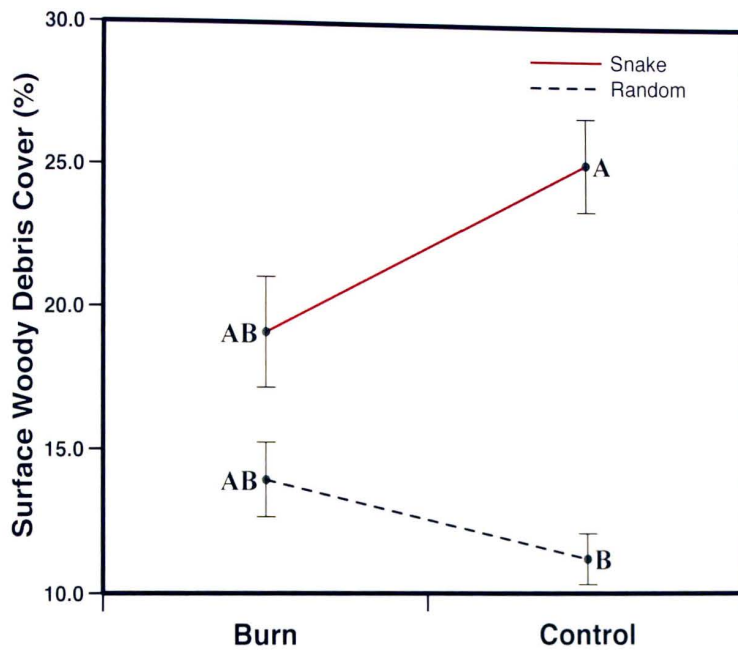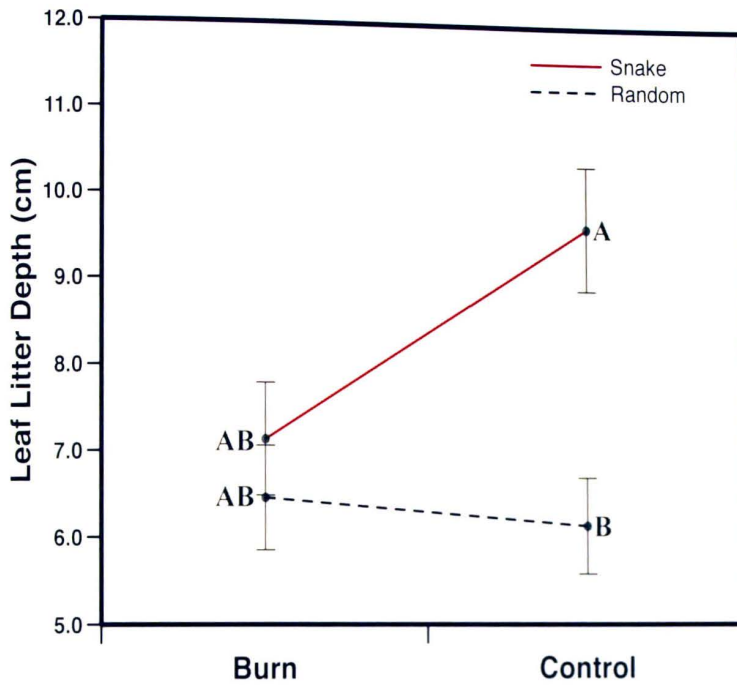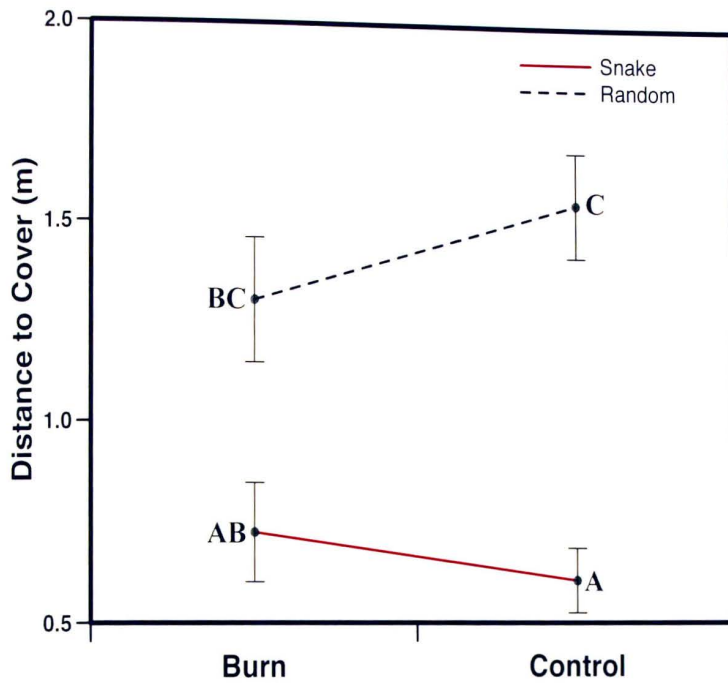**Figure 6.** Interaction plots comparing mean and standard error of distance to cover measured at snake and random locations. Mean values displaying different letters are significantly different based on repeated-measures ANOVA and post-hoc Tukey's HSD tests. Burn Snake locations were closer to cover than Control Random locations, while Control Snake locations were closer to cover than both Burn and Control Random locations (FDR adjusted P = 0.002).

Table 3. Year tracked, location of capture, number of active season days tracked, and home range size estimations using minimum convex polygon (MCP) and kernel density estimates (KDE), and mean distance moved per day of copperheads included in study. All areas are given in hectares and all distances given in meters.

Snake ID	Year tracked	Location of capture	Number of days tracked	MCP (ha)	95% KDE (ha)	50% KDE (ha)	Mean distance moved/day (m)
AGCO1	2014	Burn	123	9.2	18.4	4.5	26.6
AGCO2	2014	Control	127	10.4	29.2	8.4	20
AGCO3	2014	Burn	117	1	2.7	0.8	8.6
AGCO4	2014	Control	113	12.6	28.4	7.5	18.9
AGCO5	2014	Burn	92	3.9	8.4	1.9	13.7
AGCO6	2014	Burn	89	5.1	11.4	2.5	24.2
AGCO7	2014	Control	73	3	9.9	2.8	19.9
AGCO8	2014	Control	80	6.3	19.6	4.2	14
AGCO9	2014	Control	64	3.3	11.2	2.2	18.7
AGCO10	2014	Control	69	4.3	17.9	4.8	22.1
AGCO14	2015	Control	78	0.9	2.9	0.6	5.5
AGCO15	2015	Control	85	2.7	8.7	2.2	6.8
AGCO16	2015	Control	85	4.4	15.7	3.8	11.8
AGCO1	2015	Burn	123	3	8.7	2.3	7.3
AGCO2	2015	Control	169	16.7	44.1	11.5	17.1
AGCO4	2015	Control	169	31.2	70.5	15.1	23.3
AGCO6	2015	Burn	169	8.8	20.1	3.6	14.8
AGCO9	2015	Control	127	4.7	13.3	3.3	7

Table 4. Results of general linear model with site (Burn vs Control) as the main effect, individual snake and year tracked as random effects, and duration of active season radio-tracking used as a covariate. Least square means are reported, as well as significance of year (2014 or 2015) and duration of active season radio tracking.

Home Range Estimate	Burn		Control		Random Effect (Year)	Covariate (Duration of Tracking)	Treatment (Burn vs Control)
	Mean	SE	Mean	SE	P	P	P
MCP (ha)	2.9	2.6	9.3	2.0	0.64	0.002	0.04
95% KDE (ha)	6.5	5.7	24.7	4.5	0.62	0.0006	0.008
50% KDE (ha)	1.2	1.5	6.1	1.3	0.56	0.0001	0.003

Chapter VI

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