# Habitat Selection and Movement Patterns of Copperheads (*Agkistrodon contortrix*) in Fire-altered Landscapes

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*Abstract.*—Fire can alter habitats available to wildlife through modification of structural and micro-climatic characteristics. Because of their reliance on behavioral thermoregulation and crypsis, reptiles can be especially influenced by fire-induced habitat alterations. Copperheads (*Agkistrodon contortrix*) are a widely distributed snake species found throughout the eastern USA in a variety of habitats. Previous studies suggest that abundance of Copperheads may decrease after fire events. To investigate the specific drivers influencing potential changes in abundance, we radio-tracked 13 adult male Copperheads from burned and unburned habitats in an oak-hickory forest in western Kentucky. We tracked Copperheads for two consecutive annual active seasons (May-October) and we calculated home ranges using minimum convex polygons (MCP) and fixed kernel density estimation (KDE). We assessed movement patterns by estimating distances moved per day. At each Copperhead location, we recorded a suite of structural and environmental habitat variables and we paired each location 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 accumulated leaf litter and downed woody material. There was no difference between distances moved per day of Copperheads in burned and unburned areas, but MCP and KDE home ranges were significantly larger in unburned habitats than those in burned. The results of this study suggest that landscape alterations resulting from prescribed fire changes the manner in which Copperheads interact with their environment.

*Key Words.*—home range; movement; prescribed fire; snakes; spatial ecology

## Introduction

Disturbances are a natural part of ecosystem succession and functionality (White 1979; Sousa 1984), and 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 wide diversity of species, resulting in greater niche diversity (Bazzaz 1975; Tews et al. 2004). For some species, a 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).

The magnitude of fire-induced impacts depends both on fire frequency and intensity (DeBano et al. 1998). Low-intensity fires of moderate frequency can modify the landscape through reduction of leaf litter and downed woody material and can increase the growth of dense thickets of woody stems (Peterson and Reich 2001) and understory herbaceous plants (Hutchinson et al. 2005). Conversely, high-intensity fires are often catastrophic, resulting in die-offs of entire stands, eliminating canopy

cover and forest structure complexity (Vose et al. 1999). Increased exposure to solar radiation can then result in increased soil temperature and evapotranspiration, and reduced soil moisture (Iverson and Hutchinson 2002).

As a result of a warming trend beginning approximately 10,000 YBP, much of the southeastern United States underwent a periodic cycle of fires ignited by lightning strikes (Abrams 1992; Waldrop et al. 1992). There is also evidence of fire being used consistently as a land management tool by pre-Columbian Native Americans throughout much of southeastern USA (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 practice (Pyne 1982; Stephens and Ruth 2005). Only recently have land managers in the southeastern U.S. started using prescribed fire as a technique to mimic historic wildfire regimes and increase local species diversity (Pyne et al. 1996).

Wildlife responses to fire-altered landscapes have 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 studied, but the majority of previous work has focused on changes in species abundance and diversity in post-fire landscapes (Mushinsky 1985; Perry et al. 2009; Sutton et al. 2013; Hromada et al. 2018). It is likely that many of these changes in abundance and diversity are driven by the alteration of species-specific habitat suitability in response to fire.

Copperheads (*Agkistrodon contortrix*) are geographically widespread viperid snakes that are typically considered habitat generalists where they occur in the southeastern U.S. (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). We investigated differences in habitat selection and movements of Copperheads in fire-altered and fire-suppressed landscapes. Because some previous studies suggest a positive relationship with unburned habitat (Jones et al. 2000; Sutton et al. 2017), we predicted that Copperheads would select habitats most similar to those available in fire-suppressed areas and that movements would be greater and more frequent in fire-altered areas.

## Materials and Methods

*Study site.*—Our study site was located at Land Between the Lakes National Recreation Area (LBL) in Trigg County, Kentucky, USA. 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, led 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 y (Franklin 1994). To improve recreation opportunities and restore historic oak-savanna habitat, prescribed fire was recently adopted as a land management tool throughout LBL. In April 2007 and again in September 2010, an area of approximately 1,000 ha (Franklin Creek Burn Area) was burned using a helicopter to drop plastic incendiary spheres filled with potassium permanganate (see Howey 2014 for more detailed description of study site and burn methods). Although frontal fire intensity was not measured at the time of either burn, the controlled nature of prescribed fires and the generally low slope angle of the sites suggests that burns were likely of low intensity (Alexander 1982; Franklin et al. 2003).

*Radio telemetry.*—We initially located Copperheads via haphazard surveys of appropriate habitat and nocturnal road-cruising in the Franklin Creek Burn Area (Burn) and adjacent unburned areas within 3 km of the Franklin Creek Burn Area (Control) from May 2014 through July 2015. At time of capture, we measured snout-vent length (SVL) of each snake to the nearest 1 mm, measured body mass to the nearest 1 g, and determined sex by cloacal probing. We uniquely marked snakes by sub-dermal injection of a Passive Integrated Transponder (PIT) tag (Biomark Inc., Boise, Idaho, USA). Only male snakes were used in this study because of known intersexual differences in movements and thermal biology of temperate pit-vipers (Fitch 1960; Reinert and Zappalorti 1988; Shine et al. 2003). We transported Copperheads to a field laboratory (Hancock Biological Station), where we surgically implanted radio transmitters (SI-2, Holohil Systems Ltd., Carp, Ontario, Canada) that weighed no more than 7% of body mass. We conducted surgeries following the methods of Reinert and Cundall (1982) and allowed snakes 24–48 h to recover from surgery before release at the point of capture. Thereafter, we relocated snakes every 2–5 d from mid-May through early October (active season) between 0900–1800. At each snake location, we recorded Universal Transverse Mercator (UTM) coordinates in NAD83 datum using a GPSmap 60CSx (Garmin International Inc., Olathe, Kansas, USA). We recorded all locations to an accuracy of ≤ 3 m. Sometimes snakes crossed between habitat types (three of 13 total snakes) and we considered snakes in either Burn or Control when they spent at least 65% of their time in one of the habitat types.

*Microhabitat analysis.*—We recorded a suite of 18 environmental and habitat structural variables from a 1-m² quadrat centered on the snake location (Table 1). To avoid repeatedly disturbing snakes, we recorded habitat structural measurements after the snake had moved to another location (typically 1–3 d after initial location). To measure the habitat available for use by Copperheads, we paired each snake relocation point with a randomly selected point. We selected random points by walking a randomly selected straight-line distance (within 60 m) from the snake point at a randomly chosen compass bearing. At each random point, we measured the same suite of environmental and habitat structural variables (Table 1). We defined cover objects as any physical object a Copperhead could conceivably use to fully or partially seek refuge. We compared environmental and habitat structural variables for snake

**TABLE 1.** Environmental and structural variables collected at each snake and random location at Land Between the Lakes National Recreation Area, Kentucky, USA.

| 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 |
| Downed Woody Material Cover | % woody material 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 |

and random locations in burn and unburned areas 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 (FDR; Benjamini and Hochberg 1995).

***Movements and home range.***—We calculated distance moved per day for each Copperhead as the distance between relocations divided by the number of days elapsed between relocations. We compared distance moved per day within the burn area to those captured outside the burn area using repeated-measures ANOVA with individual snake used as the repeated (random) factor. We excluded movements of ≤ 3 m from analyses due to their overlap with location imprecision. We calculated home range size 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). We compared home range sizes of Copperheads associated with the burn area to those associated with the unburned area using a General Linear Mixed 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. We calculated home range estimation and movements using Geospatial Modeling Environment (Spatial Ecology LLC, Toronto, Canada)

and ArcGIS 10.2.2 (Esri, Redlands, California, USA). We conducted all statistical analyses using JMP version 10 (SAS Institute Inc., Cary, North Carolina, USA) and tests were considered significant using α = 0.05.

**RESULTS**

We captured four Copperheads in burn areas (Burn Snakes) and nine in unburned areas (Control Snakes). We radio-tracked five Copperheads (two Burn Snakes and three Control Snakes) during both the 2014 and 2015 field seasons. We only tracked eight Copperheads (one Burn Snake and seven Control Snakes) during either the 2014 or 2015 field seasons. We attributed this to some individuals succumbing to overwintering mortality in the winter of 2014–2015 and others were novel captures in 2015, allowing for only one season of tracking before the end of the study.

One snake in particular (AGCO5) had two of 20 observations in unburned areas for a total of six out of 92 tracking days. We feel as this individual is best classified as a Burn Snake as the vast majority of its time was spent in burned habitat. Two other snakes (AGCO3 and AGCO6) spent most of their time in burn areas, but also used unburned habitat. When space-use is compared between burned or unburned habitat (Fig. 1), we found that these snakes have either approximately equal home range area in burned and control (AGCO3) or have much reduced home range in burned habitat (AGCO6). This supports our decision to characterize
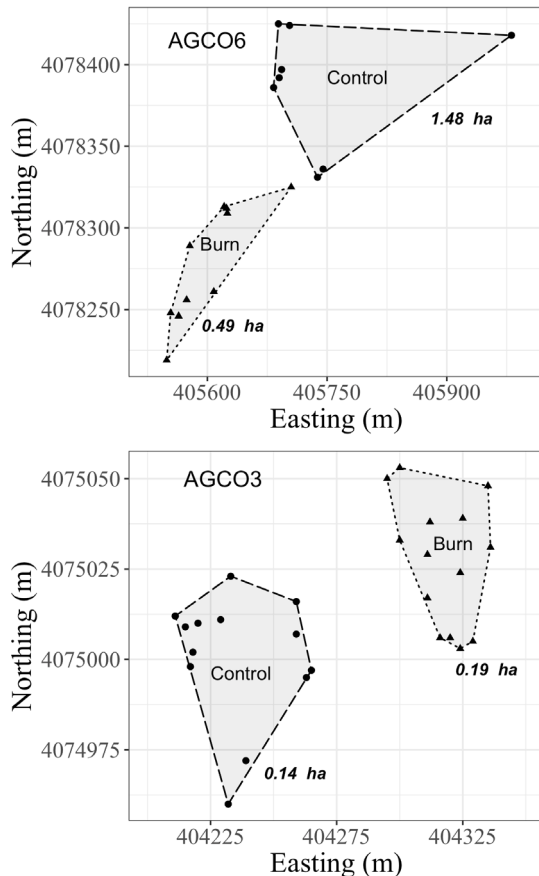
**FIGURE 1.** Minimum convex polygon (MCP) estimates of space-use by two snakes (AGCO3 and AGCO6) in burned (Burn) and unburned areas (Control) at Land Between the Lakes National Recreation Area, Kentucky, USA.

*Microhabitat analysis.*—Of the 18 environmental and structural habitat variables we recorded, five variables differed significantly among the four sampling groups (Table 2). Burn Random locations exhibited significantly higher surface temperature than Control Snake locations (FDR adjusted $P = 0.045$; Table 2). Control Snake locations exhibited greater downed woody material (FDR adjusted $P = 0.010$; Fig. 2) and deeper leaf litter (FDR adjusted $P = 0.043$; Fig. 2) than Control Random locations. Burn Snake locations exhibited greater woody stem density than both Burn Random locations and Control Random locations (FDR adjusted $P = 0.009$; Fig. 2). Burn Snake locations were closer to cover than Control Random locations, while Control Snake locations were closer to cover than both Burn Random and Control Random locations (FDR adjusted $P = 0.002$; Fig. 2).

*Movements and home range.*—We radio-tracked all Copperheads included in the analysis of movement and home range for a minimum of 64 d and located them a minimum of 11 times ($\bar{x} = 20$) during the spring and summer seasons. We found no significant difference between Burn Snakes and Control Snakes when comparing approximate distances moved per day ($F_{1,17} = 0.030$, $P = 0.876$. Home range sizes varied by individual, and overall KDE home range sizes were larger than those measured via MCP (Table 3). The duration of active season radio-tracking had a significant effect on home range size (MCP $P = 0.002$, 95% KDE $P < 0.001$, 50% KDE $P < 0.001$; Table 4), while year tracked did not (MCP $P = 0.643$, 95% KDE $P = 0.626$, 50% KDE $P = 0.564$; Table 4). After controlling for the significant effect of tracking duration (model covariate), home ranges of Control Snakes were significantly larger than those of Burn Snakes for all home range estimators (MCP $r^2 = 0.66$, $F_{1,17} = 5.690$, $P = 0.040$; 95% KDE $r^2 = 0.60$, $F_{1,17} = 11.92$, $P = 0.008$; 50% KDE $r^2 = 0.70$, $F_{1,17} = 19.53$, $P = 0.003$; Table 4).

these individuals as Burn Snakes. We were unable to use a mixed-effect model to control for the few instances in which snakes switched between burned and control areas due to the low frequency of those occurrences (Gelman and Hill 2007).
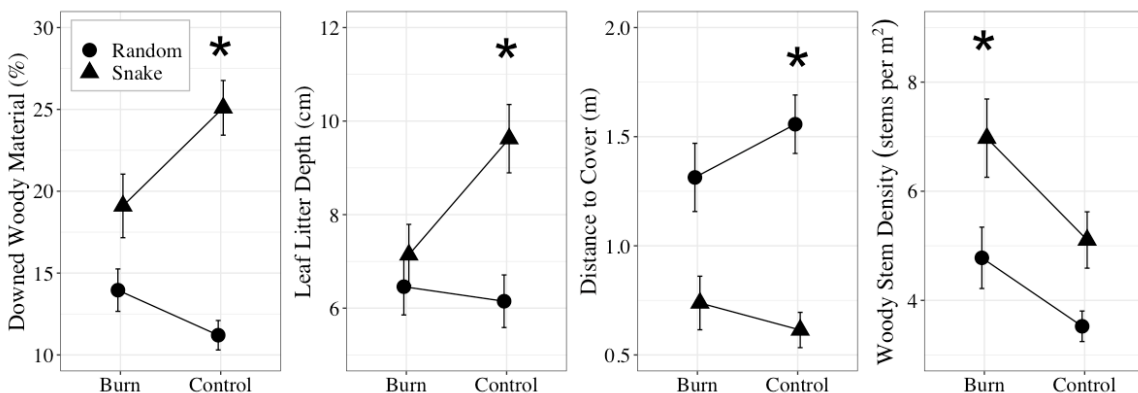


**FIGURE 2.** Interaction plots comparing means (± one standard error) of habitat features measured at snake and random locations in both burned and unburned habitats at Land Between the Lakes National Recreation Area, Kentucky, USA. Asterisks (*) indicate significant (Tukey's HSD) differences between snake and random locations within Burned or Control (unburned) habitat.

**TABLE 2.** Least square mean values and standard error (SE) of environmental and structural habitat variables measured at snake and random locations at Land Between the Lakes National Recreation Area, Kentucky, USA. Least square mean values having different superscripts are significantly different from each other based on repeated-measures ANOVA and post-hoc Tukey's HSD tests. For each $F$ test, dfs were 3 and 430. *P*-values were adjusted to control for false discovery rate (FDR). Variables that differed significantly among groups are in bold.

| Variable | Burn Snake (n = 79) Mean | SE | Control Snake (n = 138) Mean | SE | Burn Random (n = 75) Mean | SE | Control Random (n = 138) Mean | SE | $F$ | $P$ | FDR adj $P$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Ambient Temperature | 27.9[A] | 0.4 | 27.0[A] | 0.3 | 28.1[A] | 0.4 | 26.9[A] | 0.3 | 2.81 | 0.072 | 0.145 |
| **Surface Temperature** | **28.1[AB]** | **0.6** | **26.7[B]** | **0.4** | **29.5[A]** | **0.6** | **27.7[AB]** | **0.4** | **4.87** | **0.014** | **0.045** |
| Soil Temperature | 18.4[A] | 0.3 | 17.4[A] | 0.2 | 18.4[A] | 0.3 | 17.8[A] | 0.2 | 3.28 | 0.043 | 0.123 |
| Canopy Closure | 81.9[A] | 4.2 | 84.2[A] | 3.4 | 75.6[A] | 4.2 | 80.1[A] | 3.4 | 0.88 | 0.468 | 0.596 |
| Surface Leaf Litter Cover | 42.2[A] | 5.6 | 52.2[A] | 4.8 | 44.3[A] | 5.7 | 55.1[A] | 4.7 | 2.73 | 0.054 | 0.135 |
| **Downed Woody Material** | **18.4[AB]** | **2.9** | **24.9[A]** | **2.4** | **16.2[AB]** | **3.1** | **11.1[B]** | **2.4** | **5.86** | **0.002** | **0.010** |
| Surface Herbaceous Cover | 23.6[A] | 2.6 | 15.7[B] | 2.0 | 17.6[AB] | 2.7 | 15.7[AB] | 2.0 | 2.70 | 0.061 | 0.143 |
| Surface Grass Cover | 20.3[A] | 6.1 | 10.8[A] | 5.5 | 12.5[A] | 6.2 | 19.0[A] | 5.5 | 1.68 | 0.183 | 0.275 |
| Surface Open Ground Cover | 6.20[A] | 5.6 | 6.76[A] | 5.2 | 13.1[A] | 4.6 | 16.1[A] | 4.4 | 1.04 | 0.380 | 0.535 |
| Surface Rock Cover | 5.58[A] | 4.4 | 9.16[A] | 3.7 | 19.7[A] | 3.9 | 13.7[A] | 3.5 | 2.05 | 0.129 | 0.691 |
| **Leaf Litter Depth** | **7.14[AB]** | **1.0** | **9.71[A]** | **0.7** | **6.53[AB]** | **1.0** | **6.10[B]** | **0.7** | **4.95** | **0.008** | **0.043** |
| **Woody Stem Density** | **7.08[A]** | **0.5** | **5.10[AB]** | **0.4** | **4.80[B]** | **0.6** | **3.54[B]** | **0.4** | **9.00** | **0.001** | **0.009** |
| Woody Stem Height | 2.04[A] | 0.5 | 2.67[A] | 0.4 | 0.95[A] | 0.5 | 1.65[A] | 0.4 | 2.57 | 0.095 | 0.166 |
| **Distance to Cover** | **0.72[AB]** | **0.2** | **0.60[A]** | **0.1** | **1.29[BC]** | **0.1** | **1.55[C]** | **0.1** | **11.4** | **< 0.001** | **0.002** |
| Cover Height | 23.9[A] | 4.0 | 26.5[A] | 3.1 | 23.0[A] | 4.0 | 21.1[A] | 3.1 | 0.52 | 0.672 | 0.757 |
| Cover Length | 495[A] | 60 | 528[A] | 45 | 502[A] | 61 | 440[A] | 45 | 0.67 | 0.583 | 0.692 |
| Distance to Overstory Tree | 3.66[A] | 0.6 | 3.72[A] | 0.5 | 3.57[A] | 0.6 | 3.23[A] | 0.5 | 0.21 | 0.897 | 0.949 |
| Distance to Understory Tree | 1.59[A] | 0.4 | 1.44[A] | 0.4 | 1.64[A] | 0.4 | 1.74[A] | 0.4 | 0.13 | 0.949 | 0.949 |

## DISCUSSION

The results of this study suggest that landscape alterations resulting from prescribed fire management changes the manner in which Copperheads interact with their environment. Ambient and below-ground soil temperatures did not differ among burned and unburned sampling locations, but differences in ground surface temperatures suggest that Copperheads select cooler locations within the landscape and that the forest floor of burned areas is warmer than that of unburned areas. 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 cover objects for 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 select locations with more downed woody material and deeper leaf litter, while Copperheads in burned areas select locations with a high density of woody stems. This observed variation in cover selection might be representative of a differing availability of diurnal retreat sites in burned and unburned areas. Our field observations during this study support this assumption, with Copperheads in unburned areas often seen associated with piles of leaves and downed woody material adjacent to 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*).

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 frequently used in studies of snake movement (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 path of the animal. 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

**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 (*Agkistrodon contortrix*) included in study at Land Between the Lakes National Recreation Area, Kentucky, USA. All areas are given in hectares and all distances given in meters. The abbreviation SVL = snout-vent length and MDMD = mean distance moved per day.

| Snake ID | SVL (mm) | Year Tracked | Location | Days Tracked | MCP (ha) | 95%KDE (ha) | 50%KDE (ha) | MDMD (m) |
|---|---|---|---|---|---|---|---|---|
| AGCO1 | 703 | 2014 | Burn | 123 | 9.20 | 18.4 | 4.5 | 27 |
| AGCO2 | 745 | 2014 | Control | 127 | 10.4 | 29.2 | 8.4 | 20 |
| AGCO3 | 795 | 2014 | Burn | 117 | 1.00 | 2.70 | 0.8 | 9 |
| AGCO4 | 725 | 2014 | Control | 113 | 12.6 | 28.4 | 7.5 | 19 |
| AGCO5 | 885 | 2014 | Burn | 92 | 3.90 | 8.40 | 1.9 | 14 |
| AGCO6 | 814 | 2014 | Burn | 89 | 5.10 | 11.4 | 2.5 | 24 |
| AGCO7 | 1000 | 2014 | Control | 73 | 3.00 | 9.90 | 2.8 | 20 |
| AGCO8 | 870 | 2014 | Control | 80 | 6.30 | 19.6 | 4.2 | 14 |
| AGCO9 | 731 | 2014 | Control | 64 | 3.30 | 11.2 | 2.2 | 19 |
| AGCO10 | 740 | 2014 | Control | 69 | 4.30 | 17.9 | 4.8 | 22 |
| AGCO14 | 730 | 2015 | Control | 78 | 0.90 | 2.90 | 0.6 | 6 |
| AGCO15 | 612 | 2015 | Control | 85 | 2.70 | 8.70 | 2.2 | 7 |
| AGCO16 | 705 | 2015 | Control | 85 | 4.40 | 15.7 | 3.8 | 12 |
| AGCO1 | 722 | 2015 | Burn | 123 | 3.00 | 8.70 | 2.3 | 7 |
| AGCO2 | 745 | 2015 | Control | 169 | 16.7 | 44.1 | 11.5 | 17 |
| AGCO4 | 725 | 2015 | Control | 169 | 31.2 | 70.5 | 15.1 | 23 |
| AGCO6 | 814 | 2015 | Burn | 169 | 8.80 | 20.1 | 3.6 | 15 |
| AGCO9 | 737 | 2015 | Control | 127 | 4.70 | 13.3 | 3.3 | 7 |

60%. Based on data collected during telemetry studies of four ecologically distinct species of African snakes, 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 d) did not adequately represent individual movement differences between treatments.

Copperheads in this study exhibited smaller home ranges than those previously documented. Sutton et al. (2017) found that male copperheads used a home range averaging 12.0 ± 1.9 ha, while Smith et al. (2009) found male copperhead home ranges averaging 17.5 ± 2.7 ha. It is likely that our limited study duration and sampling frequency caused underestimates in our overall measurements of home range size of Copperheads.

Many factors have the potential to influence spatial habitat use. In snakes, intrinsic factors, such as body size, body condition, and sex (Smith et al. 2009; Glaudas and Rodriguez-Robles 2011; Hyslop et al. 2014; Glaudas and Alexander 2016), 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 areas to acquire enough resources to execute basic life functions. Durbian et al. (2008) found that Massasaugas (*Sistrurus catenatus*) in landscapes containing high proportions of less suitable habitat (closed-canopy bottomland forest) had significantly larger home ranges than those in landscapes containing higher proportions of more suitable habitat (bottomland wet prairie and upland xeric prairie). Similarly, Halstead et al. (2009) found that Coachwhips (*Masticophis flagellum*) using higher proportions of preferred habitat type (Florida scrub) exhibited significantly smaller

**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 at Land Between the Lakes National Recreation Area, Kentucky, USA.

| Home Range Estimate (ha) | Burn | | Control | | Random Effect P (Year) | Covariate P (Tracking Duration) | Treatment P (Burn vs Control) |
|---|---|---|---|---|---|---|---|
| | Mean | SE | Mean | SE | | | |
| MCP | 2.9 | 2.6 | 9.3 | 2.0 | 0.643 | 0.002 | 0.040 |
| 95% KDE | 6.5 | 5.7 | 24.7 | 4.5 | 0.626 | < 0.001 | 0.008 |
| 50% KDE | 1.2 | 1.5 | 6.1 | 1.3 | 0.564 | < 0.001 | 0.003 |

home ranges than those using greater proportions of less preferred habitat types (flatwoods and wetlands). Assuming that smaller home range size is reflective of greater habitat suitability in our study, we suggest that burn areas may be more suitable habitat for Copperheads than unburned areas. 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 influences mediating movement behaviors in snakes (Baxley and Qualls 2009; Halstead et al. 2009; Hoss et al. 2010; Kapfer et al. 2010). A study conducted at this same site suggest that during most of the spring and summer, Copperheads do not display overt thermoregulatory behaviors (Mueller and Gienger 2019) and are therefore likely not basing movement behaviors around assessing thermoregulatory opportunities during the time of the year when our study was conducted. 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 diurnal retreat locations, Copperheads in burned areas may not need to travel far to find appropriate refugia. Because unburned areas have reduced mid and understory vegetation, Copperheads in those areas may be forced to travel farther to find cover in the form of leaf and downed woody material piles.

It is also likely that refuge type and availability are not the only factors influencing Copperhead movements at these locations. Although dietary generalists, previous studies in this region have found that the majority of Copperhead diet is composed of rodents (Garton and Dimmick 1969). Population dynamics of many rodents in forests and woodlands are primarily driven by oak mast production and availability (Ostfeld et al. 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). Prescribed fire and forest management surrogates, such as thinning, have also been found to improve mast production in certain species of oaks (Lombardo and McCarthy 2008). As a result, it is possible that the burned areas in LBL may support greater densities of mammalian prey species. 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).

Based on previous studies of abundance, we predicted that Copperheads would prefer areas unaltered by fire disturbance. Our results, however, suggest that fire-altered landscapes likely represent more suitable habitat

for Copperheads. Although seemingly contradictory, it is possible that both arguments are valid. Previous studies of post-fire Copperhead abundance, on which we based our prediction, were conducted 1–2 y 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 4–5 y after prescribed burning was implemented. The greater amount of time since the landscape was burned has allowed much of the burned area to progress into a landscape with dense thickets of shrubs, providing abundant cover for Copperheads. The persistence of such differences after habitats have begun to recover indicates that habitat alterations may have long-lasting effects on the ecology of Copperheads. When considering our results together with those of previous studies, it is likely that the frequency of landscape disturbance is similarly important as the absence of disturbance to the preferred habitats of Copperheads.

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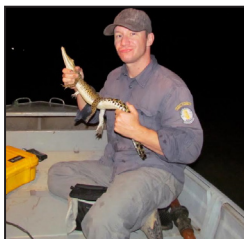


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