

Effects of a Landscape Disturbance on the Habitat Use and Behavior of the Black Racer

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The effects of disturbance, including prescribed fire, vary among species and their ability to adjust to the altered environment. Our objective was to link fire-caused habitat changes with shifts in habitat use and behavioral changes in the Southern Black Racer (*Coluber constrictor priapus*). We compared habitat availability between burned (experimental) and unburned (control) plots and used radio telemetry to evaluate snake behavior and habitat use. The numerical abundance of *C. constrictor* in burned habitat was nearly twice that in the control. In both treatments, *C. constrictor* was associated with areas that were more open, had less canopy cover, more new vegetative growth, and less, shallower leaf litter. However, the availability of these habitats was greater in the burn treatment. Snakes were more surface active in the burn treatment and tended to be more arboreal in the control treatment. Differences in available habitat may have caused an increase in surface activity in the burn treatment, which could have biased detection rates and created higher apparent abundance in the burned treatment. Females moved more often in the control treatment, which may be due to a lack of preferred thermal habitat and reproductive thermoregulatory demands. Ultimately, fire changed habitat availability and altered the movement rates and behavior of *C. constrictor* causing ecological effects that may not be detected when researchers only compare abundance.

SPECIES may respond differently to disturbance events based on how that disturbance changes the habitat availability within the landscape. Each species is adapted to particular habitat (Hutchinson, 1956; Endler, 1986), which may include food, water, cover, and nesting areas. As availability of preferred habitat changes, animals may alter their behavior and habitat use (i.e., interactions with the landscape) in response to changes in refuge from predators (Lancaster, 1996; Watling and Norse, 1998; Vickery et al., 2001), thermal stresses (Huey, 1974; Currylow et al., 2012), modification of food resources (Wunderle et al., 1991; Sekercioglu et al., 2002), and nesting habitats (Kingsford, 2000; Kolbe and Janzen, 2002; Chace and Walsh, 2006). Population sizes (i.e., abundances) may not change immediately following a disturbance, but how a species interacts with its landscape may differ and lead to changes in body condition and detection by predators, competitors, and potential mates (Fenner and Bull, 2007; Lindenmayor et al., 2008; Douglas, 2010). Ultimately, continuous long-term population studies may detect (Turner et al., 2003) changes in population dynamics, but these long-term studies are typically not logistically or fiscally feasible. Therefore, to better understand potential long-term effects of a disturbance, short-term studies should incorporate ecological effects of the disturbance on the focal species.

Prescribed fire is a popular forest management technique that mimics a natural disturbance within forested landscapes. Low-intensity prescribed fire in the central North American hardwoods can mimic wildfire and historical anthropogenic burning (Nowacki and Abrams, 2008; Taft, 2009; Guyette et al., 2012). Prescribed fire creates more open stands and generally benefits grasses, herbaceous species, and fire resistant and resilient trees such as oaks (Douglas, 2010; Brose et al., 2014). Further, an increase in oak and grass species has positive trophic consequences for some small mammal and bird species (e.g., rodents and passerines, McShea, 2000; Clotfelter et al., 2007). The increase in prescribed fire as a forest management tool requires under-

standing the cascading ecological effects brought on by habitat changes and their impact on ectothermic animals.

The response of many ectothermic species to prescribed fire is poorly understood, but has important implications for the conservation and management of their populations and the ecosystems in which they live. Particularly, ectotherms require suitable habitat heterogeneity that provides the ability to effectively thermoregulate (Angilletta et al., 2002; Angilletta, 2009). Thus, ectotherm thermal dependencies intimately link them to their habitats (Christian and Tracy, 1981; Huey, 1991; Hertz et al., 1993). The tight linkage between the reptile's physiological functions and its habitat (Huey, 1982) makes them a good focal species for evaluating ecosystem changes (Beaupre and Douglas, 2009).

Most reptiles survive prescribed fire events relatively unscathed (Withgott and Amlaner, 1996; Rudolph and Burgdorf, 1997; Rudolph et al., 1998; Smith et al., 2001) and thus remain to interact with an altered landscape. Previous studies have suggested that reptile abundances increase following a prescribed fire (Means and Campbell, 1981; Russell et al., 1999; Greenberg and Waldrop, 2008), and these increases in reptile abundance are thought to reflect a response to improvements in either the vegetative (Lindenmayor et al., 2008; Perry et al., 2012; Nimmo et al., 2013) or thermal landscape (Moseley et al., 2003; Keyser et al., 2004; Greenberg and Waldrop, 2008; Matthews et al., 2010; Elzer et al., 2013). However, comparisons with unburned habitat and changes in key habitat variables have been measured in only a few studies (Lindenmayor et al., 2008; Matthews et al., 2010; Perry et al., 2012), as have habitat preferences for the reptile species of interest (Mushinsky, 1985; Brisson et al., 2003; Yager et al., 2007). Disturbance may alter the habitat availability where species can achieve their optimal operative environmental conditions (Steen et al., 2012), which can affect abundance directly or alter habitat use, behaviors, and movement rates (Huey, 1991) and thus affect perceived abundances (Driscoll et al., 2012). Consequently, fire-altered landscapes may result in

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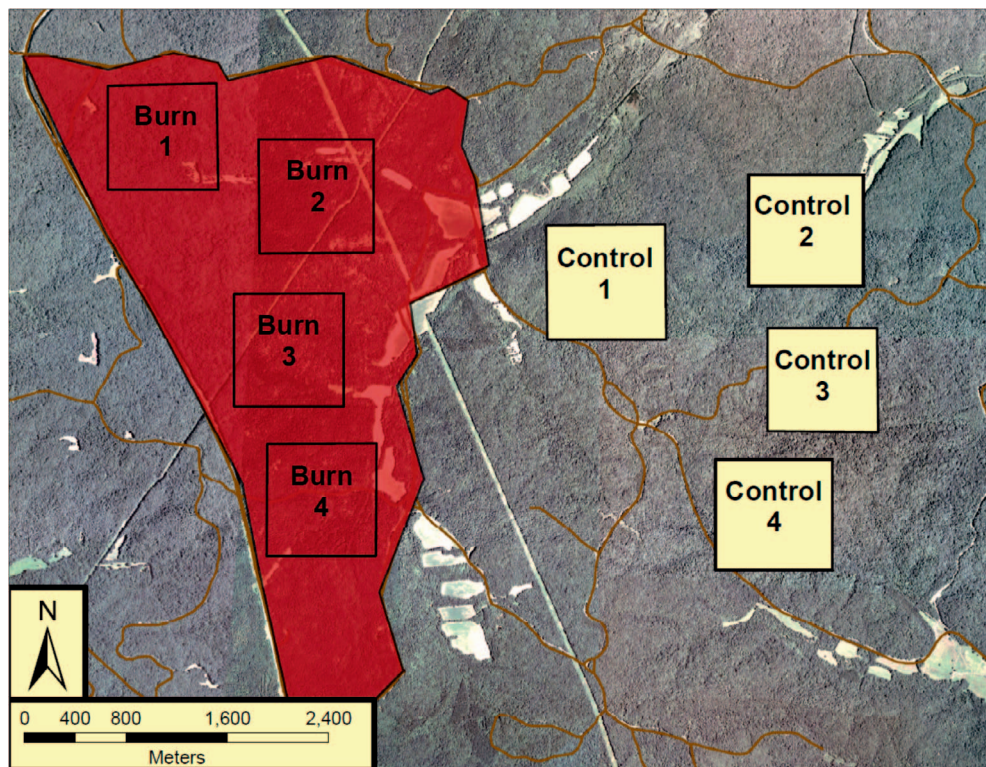


Fig. 1. Map of the study area (data available from the U.S. Geological Survey). The burn treatment is highlighted in red with the control treatment to the east. Boxes refer to study plots and a drift fence is located at the exact center of each plot. The brown lines represent dirt/gravel roads.

behavioral changes requiring a detailed understanding of these ecological effects for effective management of these populations (Lindenmayor et al., 2008; Douglas, 2010; Perry et al., 2012). We argue that short-term studies investigating the effects of prescribed fire on reptile species should focus more on the ecological effects and less on changes in abundance.

If a prescribed fire alters the behavior of a reptile species by changing the availability of habitat within the landscape, then a comprehensive understanding of the reptile-habitat interactions is required to evaluate the impact of this disturbance. Our objective was to compare the available habitat in a burned and unburned landscape with the habitat use, behaviors, and movement rates of a reptile species. We selected the Southern Black Racer (*Coluber constrictor priapus*) as a focal species because of their commonality in the study area, their generalist habitat requirements, and the large body size that would accommodate radio telemetry. We compared habitat use, movement rates, and behaviors of *C. constrictor* in both burned and unburned treatments and predicted that snakes would use particular habitat characteristics regardless of treatment and move more often when that habitat became less available.

MATERIALS AND METHODS

Study site.—We studied the response of *Coluber constrictor* to prescribed fire at Land Between the Lakes National Recreational Area (LBL) in southwestern Kentucky between April and August 2012. Prior to European settlement, the area was an oak-savanna habitat and frequently maintained by Native American-set fires (Wallace, 1992). Following European settlement and throughout the 20th century, much of the landscape was transformed by massive clear-cuts, flooding of adjacent valleys after dam construction, and the suppression of fire-related disturbances that transformed the landscape to

a mature oak-hickory forest (Wallace, 1992). Within the past 25 years, prescribed fire has been reintroduced in LBL with the management goal of transforming some landscapes back to an oak-savannah forest. Forest managers burned the 1,000-ha Franklin Creek Burn Unit (burn treatment hereafter) using aerial ignition for the first time in April 2007 and then again in September 2010. In addition to fire, the burn treatment has been disturbed by a power line and gas line that run through the center of the site (Fig. 1). The burn treatment also has a series of open meadows that are regularly maintained by USFS personnel. East of the burn treatment is an unburned area (control treatment hereafter, Fig. 1), which has not been burned since the return of fire in LBL and is not affected by power lines, gas lines, or open fields. We established four square 64 ha plots in each treatment (Fig. 1). Plots were greater than 200 m from the treatment edge and at least 500 m from another plot within the same treatment. For further description of these prescribed fires and treatments, see Howey (2014). We measured habitat characteristics and trapped at the plot level; these data were pooled within each treatment to describe differences in available habitat, habitat use, and movement rates of snakes (see below).

Habitat availability.—We established five 100 m transects and surveyed vegetation to estimate habitat availability in burn and control plots in the beginning (April), middle (June), and end (August) of the field season. We randomly determined the starting point and direction of each transect and collected data at 20 m intervals along the right-side of the transect. At each sample point, we determined ground temperature ($\pm 0.5^{\circ}\text{C}$), air temperature ($\pm 0.5^{\circ}\text{C}$), percent canopy cover, leaf litter depth (± 1 cm), and distance to nearest overstory (OST, > 7.5 cm diameter breast height [DBH]) and understory tree (UST, < 7.5 cm DBH, ± 1 m). A hand-held thermometer was used to measure air and ground

(i.e., surface) temperatures and a convex spherical crown densitometer was used to estimate overhead canopy cover. We used distance to nearest OST and UST as a proxy for tree density, assuming that mean distance to OST and UST would be less at higher densities. We also determined the percent ground cover in a 1 m² Daubenmire frame (Daubenmire, 1959), including percent leaf litter, bare ground, woody plant, forb, vine, grass, coarse woody debris (CWD), rock, and moss.

Capture and telemetry of *Coluber constrictor*.—We captured *Coluber constrictor* using a 100 m drift fence located at the center of each plot. Drift fence arrays contained a funnel trap on each side of the fence at each end of the fence and in the middle of the fence (50 m mark). We also installed pitfall traps on each side of the drift fence at 25 and 75 m marks (see Howey [2014] for more information). Drift fences were checked daily when open between April and August. We brought *C. constrictor* back to Murray State University's Hancock Biological Research Station where we measured snout–vent length (SVL $\pm$ 1 mm), tail length (TL $\pm$ 1 mm), and mass ($\pm$ 0.1 g). We determined the sex of each snake by probing the cloaca for the presence of hemipenes. Each *C. constrictor* was uniquely identified by clipping ventral scales and injecting a PIT tag subcutaneously on the posterior third of the body (Biomark, model HPT8, Boise, ID). All *C. constrictor* were released near their point of capture.

We surgically implanted (Reinert, 1992) 11 *C. constrictor* in the burn treatment and ten in the control treatment with radio transmitters (model R1680, 3.6 g, Advanced Telemetry Systems, Isanti, MN), which were less than 5% of the snake's total body mass. Snakes recovered in the laboratory for one week following surgery before they were released at the point of capture. If a snake died during this study, we assumed predator-induced mortality if the animal was found completely intact with only the head removed (typical of raptor attacks, Farallo and Forstner, 2012). Each snake was radio-located every 2–4 days. Upon locating each animal, we recorded the position/behavior of the animal (moving, basking, underground, under leaf litter, in a log, or arboreal), the Universal Transverse Mercator (UTM) coordinates, and the associated habitat characteristics. We grouped “moving” and “basking” behaviors as “surface active” due to the difficulty of determining if a snake was basking or had stopped in the open after detecting the researcher's presence; additionally, both behaviors exposed snakes to predators. We also grouped “underground,” “under leaf litter,” and “under log” as “under structure” because of low counts for the latter two behaviors. In addition to “surface active” and “under structure,” we kept arboreal behaviors separate due to the uniqueness of this behavior. We recorded all habitat data when each animal was radio-located. This may have disturbed some individuals from the point of location; however, we observed that snakes typically returned to the point of location shortly after the observer left. Habitat characteristics included all variables measured along vegetation transects (see above). We compared movement rates based on radio-locations. We compared habitat use, behavior, and movement rates between treatments because radio-tagged *C. constrictor* left study plots but remained within treatments.

Data analysis.—We compared the numerical abundance and sex ratio of *C. constrictor*, not including recaptures, between treatments using a Pearson's Chi-Square test with Yates'

continuity correction. We were unable to use mark-recapture analyses because of the low number of recaptures. Size distributions were compared using a Kolmogorov-Smirnov test. We compared body condition (residuals of an lnSVL–lnMass relationship) between treatment and sex using an ANOVA.

We compared the available habitat (1) among plots within treatments, (2) between treatments, and (3) between habitat used by snakes and habitat available within each treatment. These methods are described below in detail for each comparison. All comparisons were made using multivariate tests based on Bray-Curtis dissimilarity matrices and all statistical tests and ordinations were performed in R (R Development Core Team) using the package *vegan* (Oksanen, 2011; Oksanen et al., 2012).

We first tested for differences in available habitat among plots within treatment, which, if similar, would support grouping plots within treatment for later tests. We compared available habitat among plots using permutational multivariate analysis of variance using distance matrices (ADONIS function in package *vegan*) based on 5,000 permutations. We tested the assumption of equal dispersion using a permutation test for homogeneity of multivariate dispersions (*permutest* function in package *vegan*). We generated 95% confidence (CI) ellipses (*ordiellipse* function in package *vegan*) within a nonmetric multidimensional scaling (NMDS) ordination to determine which plots differed from one another; we interpreted non-overlap among CI ellipses as significant differences (Oksanen et al., 2012). If we detected no difference *within* a treatment, we grouped plots within treatment for sequential habitat availability/habitat use comparisons.

After gaining support to group plots within treatment, we compared available habitat characteristics between burn and control treatments using the same methods described above. Additionally, we correlated habitat characteristics to the ordination using Spearman Rank correlations which allowed us to visually interpret how available habitat differed between treatments.

Last we compared the available habitat and habitat used by *C. constrictor* in both treatments to determine (1) if habitat used by *C. constrictor* differed between treatments and (2) if habitat used by *C. constrictor* differed from what was available within each treatment. To avoid pseudoreplication within individuals, we pooled observations for each snake so that each individual was only represented once within the ADONIS and NMDS ordination. We acknowledge that this reduces the variability found within individual snakes, and thus we ran a separate ADONIS and NMDS ordination using *all* observations to determine if results were similar (included as Supplemental Material, see Data Accessibility). We tested for differences in dispersion and then compared all four groups (available habitat and habitat used by snakes in both treatments) using an ADONIS and visual comparison of differences among 95% CI ellipses for each group. Habitat characteristics were correlated to the NMDS ordination plot using Spearman Rank correlations. When snakes were arboreal, we omitted habitat used from analyses because habitat characteristics being used by snakes and available habitat could not be measured in the canopy.

We compared snake behavior (“surface active,” “under structure,” and “arboreal”) between treatments and sex using a generalized linear mixed-effect model (*lme4* package in R). We were unable to compare the use of all three behaviors in one model (multinomial mixed-effect model) due to an

Table 1. Mean ($\pm$ SD) mass (g) and snout–vent length (mm) for male and female *C. constrictor* captured in the burn and control treatments. The greater mass and snout–vent length of females in the control treatment was because few younger females were captured in the control. With the exception of females in the control treatment, individuals were similar for length and mass.

	Mass (g)	Snout–vent length (mm)
Control treatment		
Female	289.4 $\pm$ 187.7	893 $\pm$ 244
Male	157.2 $\pm$ 122.7	722 $\pm$ 229
Burned treatment		
Female	139.3 $\pm$ 81.7	703 $\pm$ 204
Male	189.5 $\pm$ 152.0	756 $\pm$ 264

unbalanced model resulting in a lack of fit. Instead we compared the use of “surface active” behaviors to “non-surface active” (arboreal and under structure grouped) with behavior as the response variable, treatment and sex as the fixed effects, snake ID as a random effect, and the exponential family being a binomial distribution. We used a logit link function given the binomial distribution for the response variable. We then compared the use of “under structure” and “arboreal” behaviors with a separate generalized linear mixed-effect model to determine differences between treatment and sex.

We compared the mean movement rate for each individual snake between sex and treatment using an ANCOVA with SVL as a covariate. We determined significance based on an alpha-level of 0.05 for all statistical tests.

RESULTS

Population characteristics.—We caught twice as many *Coluber constrictor* in the burn ($n = 39$) compared to control ($n = 21$) treatment. Sex ratios were similar between burn (20F:19M) and control (5F:16M) treatments ($\chi^2_{0.05,1} = 3.18$, $P = 0.074$, Pearson’s Chi-Square). Body condition did not differ between treatments ($F_{1,57} = 0.64$, $P = 0.427$, ANOVA) or sex ($F_{1,57} = 0.14$, $P = 0.709$, ANOVA; Table 1). Although more *C.*

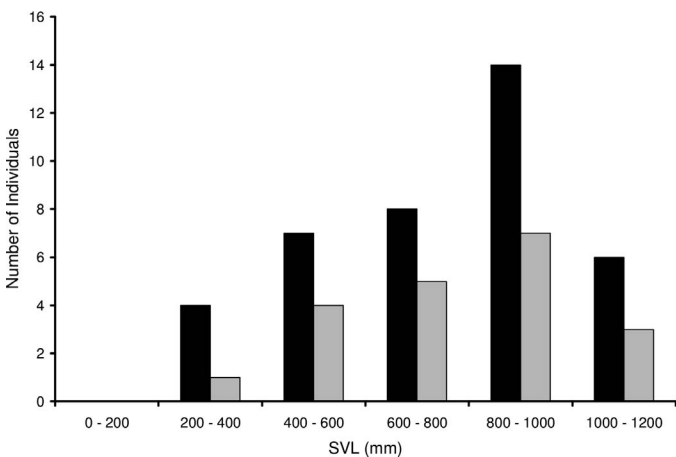


Fig. 2. Size distribution of burn and control *C. constrictor*. The number of individuals captured in burn (black) and control (gray) treatments are sorted into 200 mm interval bins for snout–vent length (SVL). Despite more *C. constrictor* in the burn treatment, the size distributions in both treatments were similar.

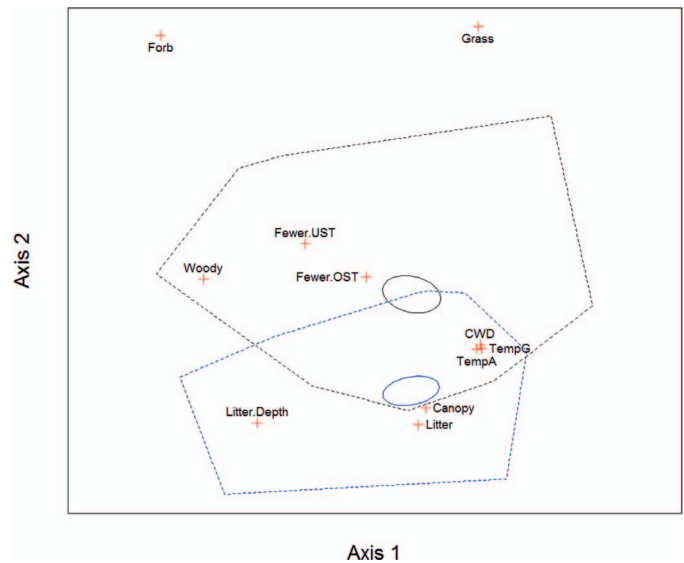


Fig. 3. Comparison of available habitat characteristics in burn and control treatments. Characteristics of available habitat in the burn (black) treatment were more associated with habitat variables toward the top of the ordination, and available habitat in the control (blue) treatment were more associated with habitat variables toward the bottom of the ordination. Hulls (dashed lines) represent the amount of variation associated with each treatment and 95% CI ellipses (solid lines) represent ordination area likely associated with true population mean. Crosses represent habitat variables correlated with ordination plot. CWD = coarse woody debris, Fewer.OST = fewer overstory trees, Fewer.UST = fewer understory trees, Litter.Depth = leaf litter depth, and TempA and TempG = air and ground temperatures, respectively.

constrictor were captured in the burn treatment, the size distribution was similar between treatments ($D = 0.14$, $P = 0.952$, Kolmogorov-Smirnov Test; Fig. 2).

Habitat availability differences within treatments.—Dispersion of habitat characteristics differed among plots ($F_{7,112} = 2.25$, $P = 0.035$, Permutest); however, this deviation was due to two vegetation transects (outliers) in one burn plot that were affected by a windthrow (a large clearing created by strong winds that knocked over trees). Although the windthrow represented available habitat, we removed both transects from further analyses because they poorly represented the burn treatment and no radio-transmitted snakes entered the windthrow. Removing the windthrow transects eliminated difference in dispersion among plots within each treatment ($F_{7,110} = 0.86$, $P = 0.540$, Permutest). Available habitat differed between burn and control plots ($F_{7,110} = 4.39$, $P < 0.001$, ADONIS), but 95% CI ellipses showed no difference among plots within treatments, thus we grouped plots within treatments for further analyses.

Habitat availability differences between treatments.—Dispersion of habitat characteristics associated with each treatment were similar ($F_{1,116} = 1.04$, $P = 0.310$, Permutest). Available habitat associated with each treatment differed ($F_{1,116} = 16.95$, $P < 0.001$, ADONIS; Fig. 3). An NMDS analysis of habitat availability resulted in a 3-dimensional ordination with 11.3% stress. The available habitat in the burn treatment was associated with a higher percentage of new vegetative growth (forbs, grasses, and woody plants) and being more open (less overstory and understory trees) as compared to the control treatment, which was associated

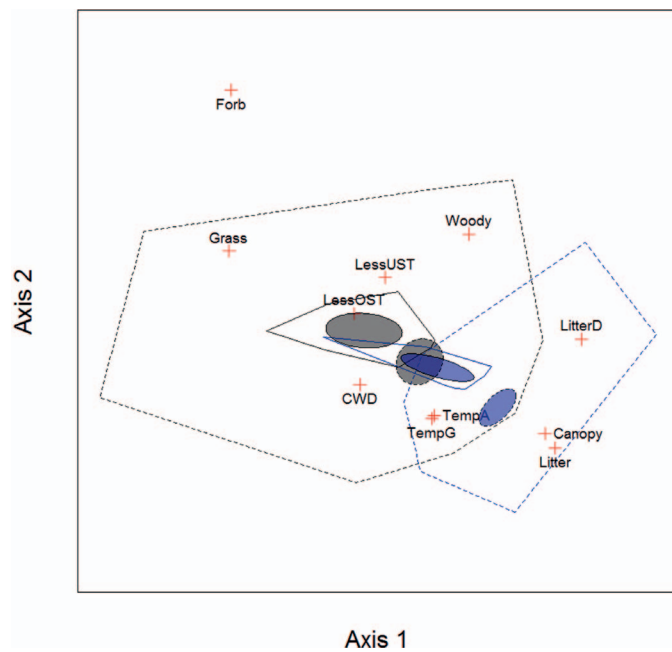


Fig. 4. Comparison of habitat use of *C. constrictor* and available habitat within each treatment. Habitat used by snakes in each treatment differed from available habitat characteristics for each treatment and available habitat differed between treatments. Characteristics of available habitat (dashed lines) and habitat used by *C. constrictor* (solid lines) in burn (black hulls and ellipses) and control (blue hulls and ellipses) treatments. Hulls represent variation of each group and ellipses (smaller, filled polygons) represent 95% CI. Non-overlap between ellipses suggests significant differences. Habitat characteristic codes are the same as Figure 3.

with a higher percentage of canopy cover, leaf litter, and deeper leaf litter depths (Fig. 3).

Habitat use.—We radio-tracked three females and eight males in the burn treatment and six females and four males in the control treatment. By the end of the summer, predators had killed five snakes in the burn treatment and one in the control treatment, which resulted in 220 and 199 radio-locations in the control and burn treatments, respectively. NMDS analysis of habitat used by snakes and habitat availability in treatments resulted in a 3-dimensional ordination with 11.7% stress. We failed to meet the ADONIS assumption of equal dispersion among groups ($F_{3,135} = 4.08$, $P = 0.008$, Permutest), so we compared available habitat and habitat used by snakes in burn and control treatments via the 95% CI ellipses. Ordination results were similar when individual observations were pooled or analyzed separately (Supplement 1).

Habitat used by *C. constrictor* differed between treatments and from available habitat in both treatments (Fig. 4, see Supplement 2 for Spearman Rank correlation values). Similar to the previous analysis (Fig. 3), the available habitat in the burn treatment was associated with more new vegetative growth (Figs. 4, 5) and fewer trees (Figs. 4, 6C), while the available habitat in the control treatment was associated with greater amounts of canopy cover, leaf litter, and deeper leaf litter depths (Figs. 4, 6A, B, see Supplement 3 Table for summary of data). Snakes used habitat with characteristics more similar to available habitat in the burn treatment (Fig. 4): open areas with more new understory vegetative growth. Habitat used by snakes in the burn treatment was further up

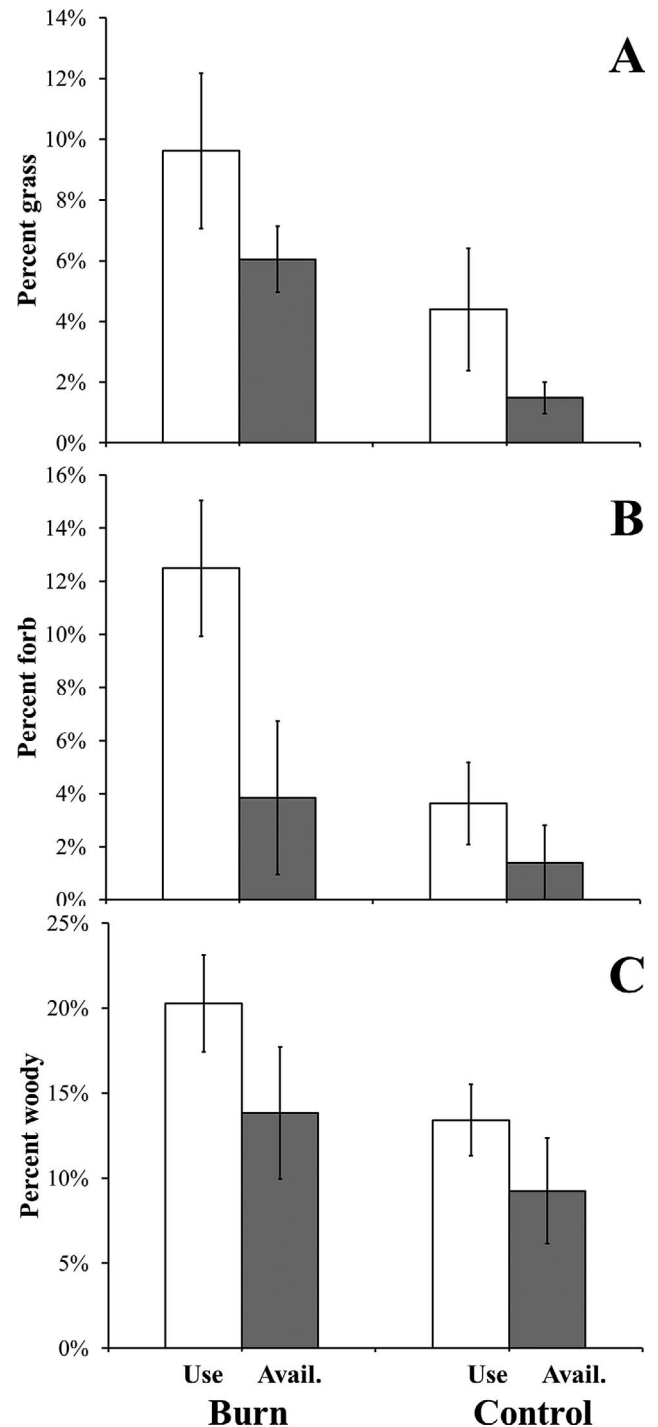


Fig. 5. Snakes used habitat (unshaded bars) that contained a greater percentage of grasses (A), forbs (B), and woody plants (C) than what was available (shaded bars) within burn and control treatments. Comparisons show means $\pm$ 2SE.

and to the left in the ordination space (Fig. 4), suggesting that as specific habitat characteristics associated with the burn treatment became more available, the species took advantage of these characteristics and used them more often (Supplement 3 Table).

Snake behavior and movement.—Snake behaviors differed between control and burn treatments. Snakes were more “surface active” in the burn treatment than in the control (Z -value = 2.166, $P = 0.030$, GLMM; Fig. 7). There was no

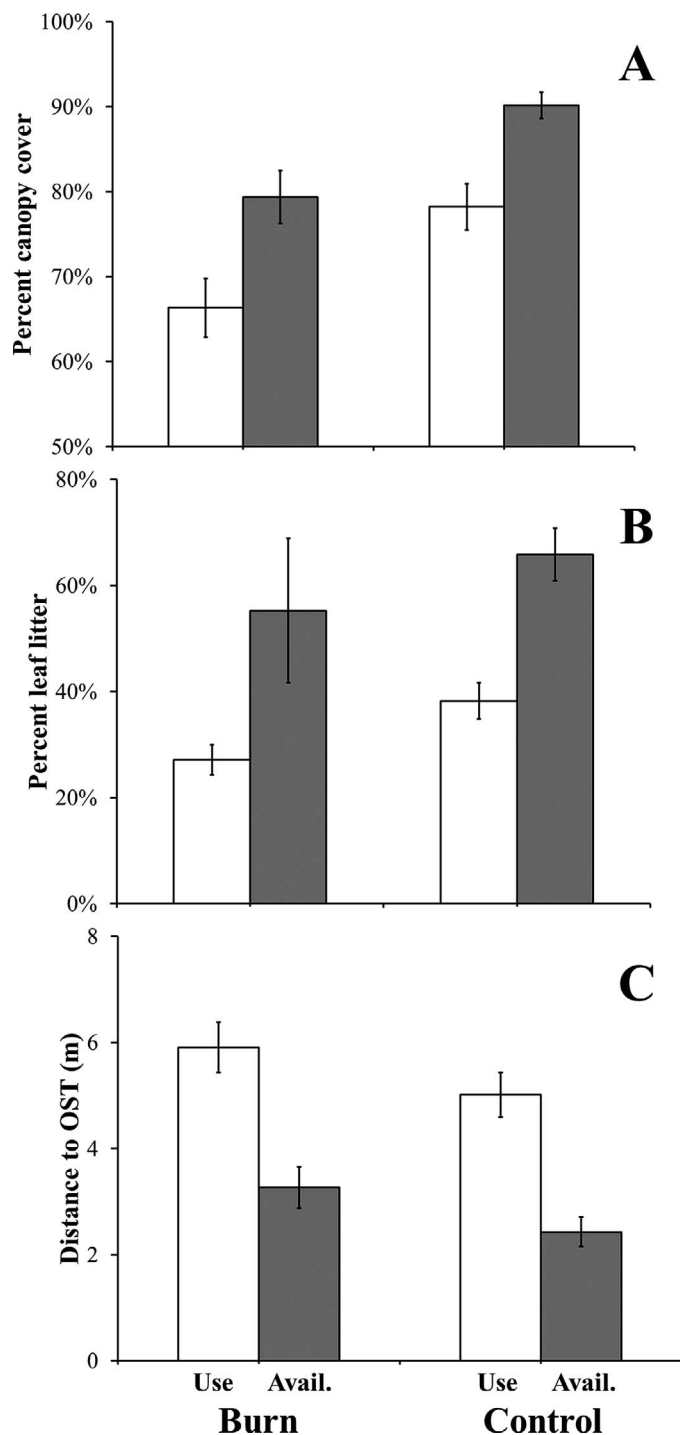


Fig. 6. Snakes used habitat (unshaded bars) that contained less canopy cover (A), less leaf litter (B), and were greater distances to overstory trees (OST; C) than what was available (shaded bars) within burn and control treatments. Comparisons show means $\pm$ 2SE.

difference in surface activity based on sex (Z -value = 0.50, P = 0.621, GLMM). We found no difference between the use of “arboreal” and “under structure” behaviors based on treatment (Z -value = 1.68, P = 0.093, GLMM) or sex (Z -value = 1.13, P = 0.259, GLMM); however, snakes tended to be more “arboreal” in the control treatment and more “under structure” in the burn treatment (Fig. 7).

There was an interaction between sex and treatment regarding movement rates ($F_{1,16}$ = 4.82, P = 0.043, ANCOVA).

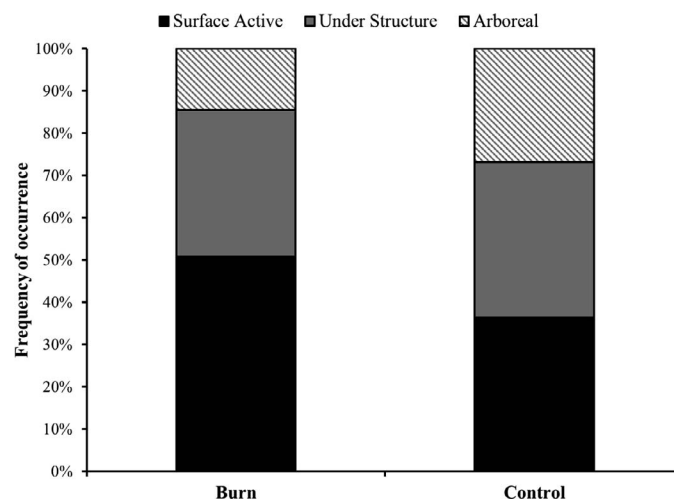


Fig. 7. Comparison of behaviors exhibited by *C. constrictor* in burn and control treatments. Snakes were surface active more in the burn treatment and arboreal or under structure more in the control treatment.

Females moved more than males in the control, and males moved more than females in the burn (Fig. 8).

DISCUSSION

Prescribed fire changed the available habitat characteristics, which affected habitat use, behaviors, and perceived abundance of *Coluber constrictor*. Burned habitat contained greater amounts of new understory vegetative growth, fewer overstory and understory trees, less canopy cover, and less leaf litter. *Coluber constrictor* used these habitats at higher rates relative to their availability regardless of treatment. Within the burn treatment, *C. constrictor* increased surface activity. Females moved less than males in the burn treatment, but more than males in the control treatment. Despite the potential benefits of prescribed burning, more of our radio-tagged *C. constrictor* were killed by predators in the burn treatment, which may be due to increased surface activity, increased predator activity, or both. The increased abundance

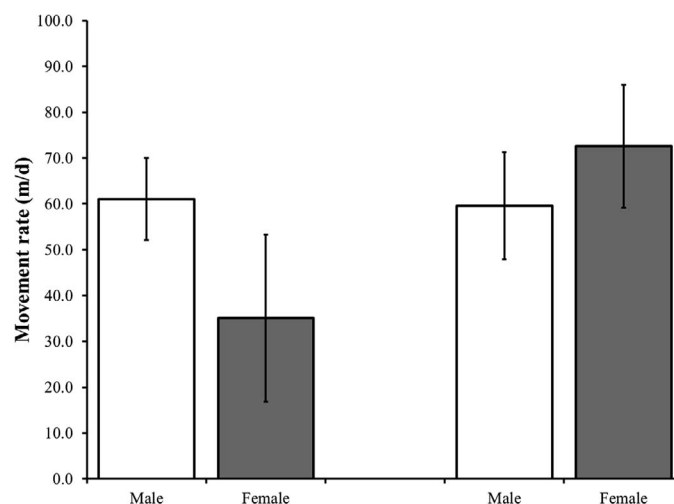


Fig. 8. Movement rates differed between treatments but were dependent upon sex. Males moved more than females in the burn treatment, and females moved more than males in the control treatment. Male movement rates did not appear to differ between treatment. Comparisons show means $\pm$ 2SE.

in the burn treatment may reflect actual population sizes or may be an artifact of increased surface activity. We discuss the effects of available habitat on population characteristics, habitat use, and behaviors in more depth.

Population characteristics.—The numerical abundance of *C. constrictor* in the burn treatment was twice that of the unburned area. Size classes were similar between treatments, indicating that the increase in numerical abundance occurred evenly across all size classes. The increase could be due to higher survivorship or increased immigration into the burned treatment. However, we did not detect any immigration of radio-tagged or PIT tagged snakes from control into burn treatments. Nevertheless, it is important to note that many of the snakes were captured with our drift fences in the center of plots and well within treatment boundaries. Thus, radio-tagged snake home ranges may not have been large enough for them to travel between treatments, and additional immigration may have gone unnoticed.

Comparisons of species abundance between treatments may be justified when recapture rates are high enough to produce reliable confidence intervals. Ideally, we would have preferred to use MARK (White and Burnham, 1999) to estimate population size, survivorship, and recapture probabilities, but our recapture rates were insufficient to calculate these parameters with a high level of confidence. Additionally, other methods like N-Mixture models (Royle, 2004) would require a higher sample size at the plot level. Many previous studies failed to mark individuals (Ford et al., 1999; Radke et al., 2008; Perry et al., 2009) or accumulate enough recaptures to result in accurate abundance estimates (Moseley et al., 2003; Greenberg and Waldrop, 2008; Matthews et al., 2010). Low recapture rates are typical for snake population studies (Parker and Plummer, 1987), which frequently compare numerical abundance (number of individuals captured) to estimate treatment effects on population size. However, numerical or perceived abundance may be biased if snake behaviors differ between treatments like they did in our study. Similarly, numerical abundance may be biased if trapping effort or trap type differ between studies. For example, Cavitt (2000) documented a decrease in abundance of *C. constrictor* while Wilgers and Horne (2006) found no effect on abundance of *C. constrictor* in the same population but following separate prescribed fire events. These biases among studies further caution against the use of perceived abundance measures to determine the effect of prescribed burning on reptile populations.

Sex ratios were similar between burn and control treatments, but there was a strong trend toward a male-biased sex ratio in the control treatment and a more even sex ratio in the burn treatment. Sex ratios for *C. constrictor* favor males at birth 2:1 in Kansas and Michigan populations (Rosen, 1991; Fitch, 1999), but higher survivorship of females leads to a more even, if not slightly female-biased adult sex ratio (Fitch, 1999). Male racers move more often and over greater distances while searching for mates (Gregory et al., 1987; MacArtney et al., 1988; Carfagno and Weatherhead, 2008), which may lead to an increase in detection by predators. We detected similar increased male movements in the burn treatment, and it was in this treatment that our even sex ratios were similar to those reported for other populations (Fitch, 1999). Male movement rates were also similar between treatments, but females moved more than males in the control treatment. Interestingly, it is in our control treatment where we detected a slightly male-biased sex ratio

while female movement rates were increased. While it is possible that an increase in female movement rates led to a decrease in female survivorship, we lack the necessary data to interpret survivorship of individuals within our population.

Habitat availability.—The prescribed fire in both 2007 and 2010 caused a reduction in overall tree biomass, canopy cover, and leaf litter and increased the opportunities for new growth of grasses, forbs, and woody saplings, results consistent with other fire-habitat studies (Abrams, 1992; Iverson et al., 2008; Taft, 2009). It should also be noted that the presence of power and gas line corridors within the burn treatment would also increase open habitat. Less canopy cover and fewer overstory trees in the burn treatment was likely due to some tree mortality caused by both prescribed fires. The increase of vegetative growth in the burn treatment was likely caused by an increase in light levels and the release of stored nitrogen within the system caused by the fire. The decrease of leaf litter is attributed to their consumption by the fire.

Habitat use, behavior, and movement rates by *Coluber constrictor*.—Within both the control and burn treatment, *C. constrictor* used habitat with more new vegetative growth, less leaf litter, less canopy cover, and fewer overstory trees than what was available. These habitat characteristics that *C. constrictor* used more often in the control treatment were more available in the burned landscape and more frequently used by snakes. In Illinois, *C. constrictor* preferred edge habitat compared to forest interior (Carfagno and Weatherhead, 2006), likely because of increased thermoregulatory opportunities provided by the open canopy. Furthermore, *C. constrictor* preferred open habitat in other studies (Plummer and Congdon, 1994; Fitch, 1999), paralleling the increased use of open habitat in our burn treatment. However, *C. constrictor* will avoid open habitat when cover becomes too sparse. Klug et al. (2010) found that *C. constrictor* used habitat with higher shrub cover, which was greatly reduced following repeated prescribed burns. Similarly, fewer *C. constrictor* were captured following a prescribed fire in open grasslands within the Konza Prairie (Cavitt, 2000; Setser and Cavitt, 2003), suggesting increased raptor predation decreased snake survivorship (Wilgers and Horne, 2007). Fitch (1963) and Fitch and Shirer (1971) noted the importance of leaf litter for *C. constrictor* which may aid in concealing the snake from potential predators or provide better foraging habitat.

Prey availability and thermoregulatory opportunities likely underlie habitat use by *C. constrictor*. The main prey for *C. constrictor* includes small vertebrates and large-bodied insects (Klimstra, 1959; Fitch, 1963; Brown, 1979; Rosen, 1991), which feed on grasses, forbs, and woody seed bearing plants like oaks and are associated with burned habitats. In fact, orthopterans (e.g., grasshoppers) occur in higher abundances following a prescribed burn once new vegetative growth has colonized the landscape (Knight and Holt, 2005; Catling et al., 2010). Greater foraging success among grasses and forbs possibly drew snakes to these habitats, but we were unable to quantify feeding rates of our radio-tagged *C. constrictor*. In control sites where grasses and forbs were less available, snakes tended to shift from surface-active behaviors (basking/moving) to more arboreal behaviors. Fitch (1999) found that arboreal *C. constrictor* potentially were better at ambushing prey (e.g., katydids, cicadas, tree frogs, and birds). Although we did not measure prey availability within trees, we did

observe a greater proportion of tree frogs and insects regurgitated by arboreal snakes.

The open areas used by *C. constrictor* also provide these snakes with increased thermoregulatory opportunities. The fact that *C. constrictor* used habitat with less leaf litter may simply be an artifact of using areas with fewer overstory trees and less canopy cover. *Coluber constrictor* may have increased surface-active behaviors in the burn treatment because of greater availability of prey and suitable thermal habitat, whereas in control plots limited availability of suitable thermal habitat also restricted surface-active behaviors. The thermoregulatory drive to use these habitats is consistent with *C. constrictor* in Illinois (Carfagno and Weatherhead, 2006). When open habitat did not exist, *C. constrictor* in our study tended to become more arboreal. This arboreal behavior may reflect increased thermal opportunities within the trees that were unattainable on the ground in control sites (i.e., the forest floor may have lacked thermal heterogeneity). Shine et al. (2005) found *Thamnophis sirtalis parietalis* used more arboreal behaviors when air temperatures were warmer than ground temperatures. Perhaps *C. constrictor* sought out warmer thermal environments within the canopy when the understory was heavily shaded and cooler, as seen in the control treatment.

In previous studies, male racers were more arboreal than females (Fitch and Shirer, 1971; Plummer and Congdon, 1994), which was attributed to the smaller size of males allowing them to be more adapted to a scansorial life style. In contrast to these previous studies, both sexes used arboreal behaviors equally in our study. The females in our control treatment may have used arboreal behaviors because of a limited availability of preferred habitat on the ground. Female *C. constrictor* in Illinois used edge habitat more than males, likely due to reproductive demands of vitellogenesis or developing embryos (Carfagno and Weatherhead, 2006). If preferred thermal habitat, open habitat, or edge habitat was rare in the control treatment, and thermal characteristics were more favorable in the canopy, then this may explain why females used arboreal behaviors.

Females in the control treatment moved more than males. If preferred thermal habitat was rarer in the control treatment, then females may have increased movement rates in order to seek out rare open habitat. None of our radio-tagged females appeared to be gravid during our study. The implantation of the radio transmitter may have caused females to divert energy towards healing from surgery. Female *C. constrictor* in Michigan reproduce every year (Rosen, 1991), and vitellogenesis begins prior to hibernation. Thus reproductive demands associated with the next year may have increased the need for our females to thermoregulate during the current study, which led to increased movement rates and the use of arboreal behaviors in the control habitat where canopy cover (i.e., shade) was dominant along the forest floor.

Conclusions.—We found that snakes behaved differently in burned vs. control areas which differed in available habitat. Whereas we acknowledge that the strength of this study would be improved with multiple study sites, obtaining multiple prescribed burn sites was not feasible at LBL and, in any case, replication of burn experiments, which differ in fire behavior and effects, is not possible in a strict sense (van Mantgem et al., 2001). Because *C. constrictor* were more surface active within the burned treatment, these behavioral differences may have biased

capture rates. We found *C. constrictor* in the control treatment tended to be more arboreal, which may have further reduced detection rates and exacerbated differences in perceived abundance. However, the habitat that *C. constrictor* used within both control and burn treatments was made more available by prescribed burning. This study suggests that prescribed fire in oak-hickory forests can be used to create habitat with better thermoregulatory and foraging opportunities for *C. constrictor*. It should also be noted that differing burn regimes, timing, and burn conditions can lead to different post-fire landscape and, thus, differing responses by resident fauna. Changes in species interactions with their environment may also have cascading effects throughout their ecosystem. To understand the ecological effects of fire as a mechanism of disturbance on resident species, future studies should monitor population dynamics but also how the ecology of individuals change in response to the fire.

DATA ACCESSIBILITY

Supplemental material is available at <http://www.copeiajournal.org/ce-15-373>.

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