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Fuels Management and Habitat Restoration Activities Benefit Eastern Hognose Snakes (*Heterodon platirhinos*) in a Disturbance-Dependent Ecosystem

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Abstract.—**Eastern Hognose Snakes (*Heterodon platirhinos*) are considered a species of conservation concern in the northeast United States because of their association with rare and declining habitats such as pine barrens and shrublands. These are disturbance-dependent habitats that currently require management to persist. We studied Eastern Hognose Snakes on a pitch pine–scrub oak barren in western Massachusetts from 2008 to 2013 to describe patterns of space use, habitat selection, and survival of this species and to evaluate the effects of habitat restoration and fuels management. We monitored 12 snakes with radio telemetry during the months of May to October 2008–2010. We examined habitat use versus availability using paired logistic regression analyses in which availability was temporally and spatially explicit in relation to radio-tracked snakes' previous use location and likely movements. We found that radio-tracked snakes significantly avoided closed-canopy forests and power line corridors, and instead primarily used heavily thinned pitch pine and scrub oak barrens. Individuals that used some closed-canopy forested habitat had significantly larger home ranges compared to snakes that used only managed early-successional habitat, congruent with ecological theory that habitat quality can affect home range size. We calculated a probability of 0.61 for adult survival during a 150-d active season (95% confidence interval [CI] = 0.22–0.85), similar to other reports of adult survival for this species. We conclude that fuels reduction and habitat restoration activities, primarily heavy thinning, are increasing the amount of preferred habitat available for this threatened species.**

Fire-dependent plant communities and the species that depend on them are threatened worldwide as the result of fire suppression that inhibits the regeneration of fire-adapted species and encourages competition from fire-intolerant species (Moreira et al., 2003; Nowacki and Abrams, 2008). In the eastern United States, pitch pine–scrub oak (PPSO; *Pinus rigida–Quercus ilicifolia*) barrens are an imperiled disturbance-dependent community that has declined substantially; in some regions <10% of historical barrens remain (Motzkin et al., 1999). Additionally, when fire is suppressed in PPSO barrens, fuels accumulate to hazardous levels that pose extreme fire risk (Duveneck and Patterson, 2007; Bried et al., 2014). Pitch pine–scrub oak barrens encompass substantial portions of some of the most densely populated regions on the continent (U.S. Census Bureau, 2009). Therefore, residential developments often are adjacent to, or embedded within, the pyrogenic plant community (Gifford et al., 2010), such that the risk of human-caused ignitions and uncontrollable wildfire is high. To reduce the risk of wildfire and restore habitat, management efforts have included mowing, controlled burning that kills off fire-intolerant species, and reducing pitch pine canopy cover (Duveneck and Patterson, 2007).

The distinctive fauna of PPSO barrens includes threatened invertebrates (Wagner et al., 2003), birds (King et al., 2011; Akresh and King, 2016), and herpetofauna (Stewart and Rossi, 1981). Eastern Hognose Snakes (*Heterodon platirhinos*) are considered a species of conservation concern over much of their range in northeastern United States and are closely associated with disturbance-dependent PPSO barrens within this region (Michener and Lazell, 1989; Therres, 1999). Because Eastern Hognose Snakes prefer xeric, sandy soils with open-canopy habitat and avoid heavily forested areas (Platt, 1969; Plummer and Mills, 2000; LaGory et al., 2009), they could be dependent on open-canopy, shrubland habitat created by forest management. In other disturbance-dependent ecosystems, snakes often select managed and restored early-successional habitats (Waldron et al., 2008; Bailey et al., 2012); however, the effects of thinning and fuels control treatments on habitat selection, space use, and survival of Eastern Hognose Snakes are poorly understood.

We studied Eastern Hognose Snakes at a PPSO barrens site in western Massachusetts to understand better the effects of habitat restoration and fuels reduction, and to assist managers in the conservation of threatened snake populations. By radio-tracking snakes that were able to use adjacent managed and unmanaged areas in our study site, we assessed if snakes were more likely to use managed, early-successional habitat than closed-canopy forest. We also examined home range sizes, daily movements, and survival rates of the snake population in our managed study area to compare with previously reported parameters of Eastern Hognose Snake populations in other study areas that had relatively more canopy cover and were not specifically managed for fuels reduction (e.g., Plummer and Mills, 2000; LaGory et al., 2009). Lastly, we determined if snakes' home ranges, movements, and survival in our study site varied among snakes that used, or did not use, closed-canopy forest.

Materials and Methods

Study Site.—We conducted our study between 2008 and 2013 in the Montague Plains Wildlife Management Area, an ~600-ha site located in Franklin County, Massachusetts (42°34′N, 72°31′W; datum WGS 84). Habitats within the study area included pitch pine forest, scrub oak barrens, power line corridors, and mixed deciduous forest (King et al., 2011; Akresh, 2012). Pitch pine–scrub oak barrens are characterized by xeric, sandy soils, with a plant community dependent on fire or management activities (Motzkin et al., 1999). The Massachusetts Division of Fisheries and Wildlife has been conducting habitat restoration and fuels reduction in the PPSO barrens study site since 2000. Most scrub oak stands were mowed or burned once or twice since 2000, although stands in the northern part of the study site were not

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treated. Scrub oak stands had low tree canopy cover (<22%) with a dense shrub cover dominated by scrub oak and low-bush blueberry (*Vaccinium angustifolium*; King et al., 2011). Pitch pine and deciduous forests had a mostly closed canopy with sparse understory. Since 2004, ~50% of the closed-canopy pitch pine forest had been thinned to 40% canopy cover, creating a drastically different habitat type (King et al., 2011; Akresh et al., 2015). The treated pitch pine stands in our study site had a sparse pitch pine canopy, with shrub and ground layers of oak and other tree saplings, low-bush blueberry, Pennsylvania sedge (*Carex pensylvanica*), and other ferns and forbs. Power line corridors were managed primarily by selective herbicide applications every 4–5 yr, and were dominated by *Spiraea* species, regenerating pitch pine, and other shrubs and grasses. Some areas of urban development existed on the east side of the study site, including the towns of Lake Pleasant and Millers Falls. Mowed fire breaks and roads existed within and along the borders of the study area and two water bodies, Lake Pleasant (21.4 ha) and Green Pond (6.5 ha), were situated on the east side of the study site.

Sampling.—We attempted to capture Eastern Hognose Snakes by using funnel traps, cover boards, constrained searches, and incidental encounters. In 2008, we installed funnel traps along 10-m silt-fabric drift fences (Corn, 1994) at three points within each of the untreated pitch pine, treated pitch pine, and scrub oak habitats. We checked traps every other day from May through August 2008. We also placed two cover boards (61 × 122–cm sections of 6-mm plywood) at these same 9 points, and at 21 other points evenly divided among these three habitats. We checked cover boards three times per year between May and August, 2008–2010.

At each of the 30 sample points, we conducted constrained searches once during 2008 at which time an observer searched for 1 h within a 50 m radius area surrounding the sample point. In addition, we collected snakes incidentally between May and August, 2008–2013, primarily in treated pitch pine, scrub oak, and power line corridors during the course of this study and another study (Akresh et al., 2015).

Upon capture of most snakes, we measured mass with the use of a 1,000-g Pesola scale (±5 g), and snout–vent length and total length with the use of a meter stick (±1 cm). We determined the sex of most snakes by the length and shape of the tail (Shine et al., 1999); however, for some snakes we were unable to identify the sex. To facilitate recognition of individuals, we inserted a unique Passive Integrated Transponder (PIT) tag (12 × 2 mm, 0.06 g) into adult snakes (>100 g; LaGory et al., 2009), and between 2011 and 2013, we also marked a unique scale on the snakes with the use of a hand-held cauterizing unit (Winne et al., 2006). Between 2008 and 2010, a local veterinarian surgically implanted Holohil SB-2 radio-transmitters (10 × 20 mm, 5.2 g, expected battery life = 10 mo; Carp, Ontario) into the abdominal cavities of nongravid, larger adult-sized snakes (>150 g) following the protocol in Reinert and Cundall (1982). We monitored postsurgical snakes overnight and released them the following day at their capture location. We attempted to relocate radio-tagged snakes using Telonics T-2 receivers (Mesa, AZ) with two-element Yagi antennas every 2–3 d until the snake reached hibernaculum or died. If we lost the signal, we attempted to relocate the snake every few days throughout the remainder of the season. On average, we relocated snakes every 2.5 d (median = 2 d; 87% of relocations were ≤3 d) and recorded Global Positioning System (GPS) coordinates with the use of Garmin units (models GPS 60, GPS 76, GPSmap 60CSx, and GPSmap 62; Garmin International, Inc., Olathe, Kansas, USA) at each snake's capture and relocation sites.

Space Use Analysis.—We examined Eastern Hognose Snake home range sizes with the use of the GPS locations of radio-tagged snakes. Statistical analyses were conducted with the use of the R Statistical Program version 3.2.1 (R Core Team, 2015) and the ArcGIS program version 10.1 (ESRI, 2012). To compare our home range sizes with previously published studies (Plummer and Mills, 2000; LaGory et al., 2009), we created 100% minimum convex polygons (MCP) with the use of the adehabitatHR package in R (Calenge, 2006). We also calculated home range sizes with 95% fixed kernel utilization distributions (UD) with the use of the ks package (Fieberg, 2014; Duong, 2016) and assessed core use area by determining 50% kernel UDs for each snake. Plug-in and reference bandwidths with unconstrained bandwidth matrices provide reasonable kernel estimates when there are small numbers of telemetry fixes (Bauder et al., 2015). We used plug-in bandwidth estimates to reduce over-smoothing and to place emphasis on areas of observed use (Bauder et al., 2015), while acknowledging that home range size estimates using reference bandwidths were highly correlated with the plug-in estimates ($r = 0.97$ using 95% UDs).

For our kernel estimates, we excluded telemetry fixes where the snake was re-located in the same location over multiple days (≤1 m of the previous location; LaGory et al., 2009; Timm et al., 2014). Some of the omitted stationary telemetry fixes were not independent because we observed instances when snakes were stationary for multiple days or even weeks, perhaps due to ecdysis (Halstead et al., 2009). Nevertheless, estimates including or excluding stationary telemetry fixes were highly correlated ($r = 0.89$ using 95% UDs) and excluding stationary fixes did not affect our results when comparing among snakes' home ranges. We observed very few short movement distances (1–2 m) and most (98%) movements were >2 m. We calculated home range size for snakes that had ≥15 unique locations, consistent with the methodology used in other snake studies (LaGory et al., 2009; Martino et al., 2012). Furthermore, a small number of fixes can produce accurate home range estimates (Börger et al., 2006; Bauder et al., 2015). For snakes with ≥15 unique locations, MCP and kernel estimates were not affected by the number of unique locations or by the number of days tracked ($P > 0.10$ in all correlations). We included data for a single snake that we could not locate for about 1 mo that we credit to transmitter failure, rather than to a movement foray.

Because snakes that use a preferred habitat can have small home ranges relative to those that use both preferred and nonpreferred habitat (Halstead et al., 2009; Kapfer et al., 2010), we tested for differences in MCP size between snakes that used entirely open-canopy habitat versus those that used both open and closed-canopy forest, with the use of a Mann-Whitney *U*-test. We also tested for differences in MCP size between sexes and among years with the use of Mann-Whitney *U* or Kruskal-Wallis tests. We reported analyses of home range size using only MCPs because both 50% and 95% kernel UD estimates were highly correlated with MCP estimates (both $r = 0.99$), and analyses with kernel estimates had the same results as MCPs.

For each snake movement, we calculated a daily movement rate by dividing the Euclidean distance between the two successive locations by the number of days between them (Halstead et al., 2009; Martino et al., 2012). If the snake was stationary for multiple telemetry fixes and then moved to a new location, we included only the number of days between the last stationary telemetry fix and the relocation (Timm et al., 2014).

Given that we did not monitor snake locations hourly or daily, we note that daily movement rates are minimum estimates because snakes could have had nonlinear movements. We calculated average daily movement rates (meters/day) for each radio-tagged snake, and tested for differences between sexes and among years. We also tested if snakes that used some closed-canopy forest had different average daily movement rates compared to snakes that used only open-canopy habitat. For descriptive statistics, we report means ± SD.

Habitat Selection Analysis.—We examined habitat selection of radio-tagged snakes by comparing the habitat actually used by snakes versus the habitat that was potentially available to the snakes, based on the snakes' previous locations and likely movements (Arthur et al., 1996; Hjermann, 2000; Rhodes et al., 2005; Timm et al., 2014). Because our habitat selection approach defined snakes' available habitat in relation to where snakes were actually located, and how far snakes would likely travel, any bias in the snakes' initial capture locations did not affect the habitat selection results. We created random, available points within the study site uniquely for each telemetry relocation using a similar method as described by Timm et al. (2014). From the daily movement rates calculated for each snake relocation (see above), we examined daily movement distance distributions (meters/day) of all unique snake relocations and fit these raw data to generalized Pareto distributions (Pickands, 1975), which are right-skewed, continuous distributions that matched our data well. We fit separate distributions for males and females, because some females moved farther per day and the tail of the Pareto distribution was more extensive for females than it was for males. We determined the specific curves of the Pareto distributions by calculating the maximum-likelihood estimates of the parameter values that best fit the daily movement distance distributions of the raw data.

In the second phase of creating random, available points, we established a likely distance-moved estimate by randomly sampling a single value with replacement from the estimated generalized Pareto distribution and then multiplying the value by the number of days between a given telemetry location and the snake's subsequent relocation. Therefore, our distance-moved estimate represented the Euclidean distance that the individual snake likely would have moved during the time between its use location and its subsequent relocation. Next, we randomly sampled one movement azimuth with replacement from a uniform distribution of 0–359°, and positioned a random, available point along this azimuth heading at the calculated distance (from the previous step) from the snake's previous use location. If a random location was positioned either outside of our study area boundary or within a lake (<2% of the random locations drawn), we discarded it and drew a new location until it fell within our study area. With the use of our method that accounted for a snake's original location and the distance that a snake would likely travel, we created 100 random, available points that defined where the snake could have gone (see example in Fig. 1). The random, available points can also be considered "simulated relocations," and we used these points later in our paired logistic regression analyses to compare with the actual, observed relocations of the snakes.

We created a Geographic Information System (GIS) layer of habitat types with the use of treatment maps and aerial photos (MassGIS, 2009) by manually digitizing polygons of the following habitat types: scrub oak, treated pitch pine, power line corridors, pitch pine forest, deciduous forest, other early successional or sand pit habitat, and urban habitat (mowed lawns, buildings, etc.). We then used the habitat coverage GIS layer to assign each snake location and random point with a habitat type.

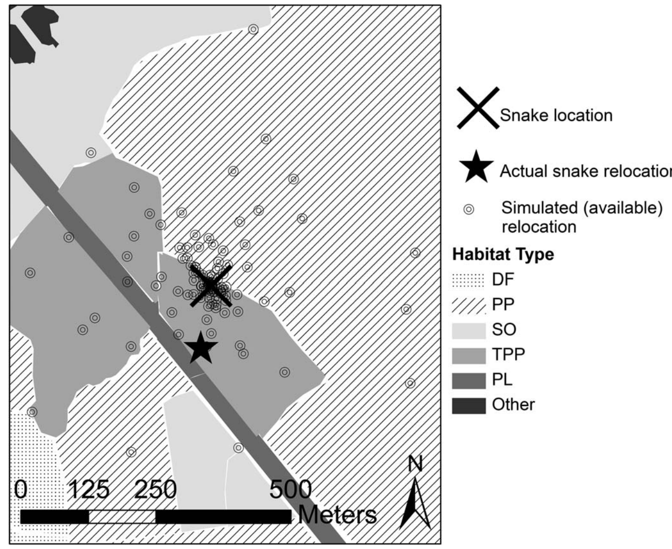

FIG. 1. An example of one movement of a radio-tagged, male snake (initially released on 5 June 2009), including one of its actual use locations that was relatively close to the forest edge (on 26 June), the snake's actual relocation (on 29 June), and the 100 simulated available, random points (or "simulated relocations") that were paired with the actual relocation. Acronyms are: DF = deciduous forest, PP = pitch pine forest, SO = scrub oak, TPP = treated pitch pine, PL = power line corridors, Other = other early successional or sand pit habitat.

We also examined actual snake locations and random points with distance to edges. We created GIS data layers of different edge types: forest versus early-successional habitat edge, urban edge, lake edge, and road edge. To condense and simplify road edge, we combined the many different types of roads found in our study site (dirt, sand, grassy, and paved roads, mowed fire breaks, roads within forest, and roads within early-successional habitat) into a single road edge category. With the use of the spatstat package (Baddeley and Turner, 2005) in R, we then measured the distance of each use and random point to the closest edge of each edge type as well as the closest distance to any edge.

We compared actual relocations versus random points with paired logistic regressions, with the use of the seven habitat variables and the five distance-to-edge variables (Compton et al., 2002). For the actual use values in the paired logistic regression, habitat types were represented as dummy variables (i.e., a use point in scrub oak habitat was given a value of 1; all other habitat variables were given a value of 0). For the 100 random, available points for each relocation, we averaged the values for each predictor variable across all 100 simulated random points and applied the result as the paired random value in the paired logistic regression analyses. By averaging the 100 simulated random points for the habitat variables, we effectively made a proportion of the number of random points in each habitat type. Finally, in preparation for paired logistic regression, we subtracted the averaged random values (where the snake could have gone) from the corresponding use values (where the snake went), for each unique snake movement. In accordance with conducting paired logistic regression, the response was set at 1 and we removed the intercept from the models (Compton et al., 2002). Given the large number of predictor variables, we first conducted variable selection by

TABLE 1. Summary statistics and home range sizes for 12 individual Eastern Hognose Snakes that were radio-tagged and tracked in our study (home range size was not computed for snakes with < 15 unique locations). MCP = minimum convex polygon. UD = utilization distribution.

Year	Sex	Mass (g)	Date released	Days tracked	Number of telemetry fixes	Number of unique locations	Mean daily movement (meters/day)	100% MCP (ha)	95% Kernel UD (ha)	50% Kernel UD (ha)	Usage of some closed-canopy forest	Notes
2008	M	155	17 Jun	115	42	41	40.5	19.31	26.46	5.54	Yes	
2008	M	160	3 Jul	67	24	23	33.4	5.67	9.13	1.46	No	Transmitter found out of snake
2008	F	350	29 Jul	73	25	24	11.4	0.84	1.27	0.24	No	
2009	F	330	21 May	145	62	48	28.9	13.28	18.97	4.62	No	
2009	M	350	5 Jun	38	17	16	32.7	2.55	4.45	0.83	No	Lost signal
2009	M	250	26 Jun	116	47	42	35.7	8.87	12.79	2.89	No	Mortality (unknown cause)
2010	F	155	6 May	53	20	16	29.9	3.04	6.42	1.36	No	Lost signal
2010	F	480	6 May	74	30	28	80.3	40.23	54.67	13.26	Yes	Mortality (depredated)
2010	F	315	12 May	103	45	33	24.0	34.38	45.96	9.02	Yes	Lost signal for a month
2010	F	435	26 May	28	12	12	11.5				No	Lost signal
2010	F	175	30 Jun	84	38	23	99.0	57.84	94.29	20.39	Yes	
2010	F	190	8 Jul	27	12	5	15.1				No	Mortality (depredated)

running single-covariate models. If the effect of the given single variable was highly not significant ($P > 0.25$), then we discarded it in further analyses.

With the use of an information-theoretic framework, we conducted an all-subsets approach comparing every possible model made from the selected remaining variables. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Akaike's model weights (ω_i) to rank the candidate models and determine the top models that best described the selection of snake use locations (Burnham and Anderson, 2002). We used model averaging with the 'MuMIn' package (Bartoń, 2014) to derive parameter estimates and CIs from the top models that were within seven AIC_c values from the best model (these top models comprised 94% of the weights of the model set). We determined significance if the odds ratios' 95% CIs did not include 1 (Timm et al., 2014).

Mark-and-Recapture and Survival Analysis.—To examine the probability of recapture, we assessed interannual recapture rates for all PIT-tagged snakes captured in 2008–2012. We also examined within-year recapture rates of PIT-tagged snakes, excluding snakes that were tracked with radio-transmitters. Because our recapture rates of PIT-tagged snakes were very low, we did not conduct more in-depth survival analyses of the PIT-tagged snakes (Cooch and White, 2015).

We estimated survival for radio-tagged snakes with the use of known-fate survival models in Program MARK (White and Burnham, 1999), run through the R package 'RMark' (Laake, 2013). We used the "nest survival" model, a specific type of known-fate survival models, because we were interested in daily survival and had "ragged" telemetry data (i.e., different individuals were sometimes monitored on different days; Cooch and White, 2015). We calculated a daily survival rate, as well as an estimated survival rate for 150 d—an approximate period for seasonal survival in our study site from emergence in late April and early May to the onset of dormancy in late September and early October. Besides the null survival model, we also examined single-covariate models to analyze differences in daily survival rates between males and females, between snakes that used or did not use closed-canopy forest, and to analyze the effect of initial weight at capture. For snakes that completely disappeared from the study site ($n = 4$, one of which the transmitter, but not the snake, was found), we assumed that the snake had survived (Weatherhead et al., 2012). There is the possibility that for these "lost" snakes, the transmitters were damaged during a predation event or moved out of the study site by a predator; however, we think the "lost" snakes were more likely the result of transmitter failure (or transmitter ejection for one snake). Nevertheless, we note that the daily survival rate from the model could be an overestimate, based on our assumptions of no mortality of the lost snakes. We defined "observation days" as those between the initiation of radiotelemetry and the onset of dormancy, death, or the last known sighting for "lost" snakes. Also, for the additional snake that we lost for a month, but then re-located, we included only those observation days when we were able to track the snake.

RESULTS

Summary Statistics.—We PIT-tagged 46 of the total 56 snakes captured. Almost all of the snakes were captured during incidental encounters; only one was captured in the funnel traps and four were captured under a discarded sheet of wood that was not deployed during our study. Of these total captures, 17 were adult males, 27 were adult females, 5 were adults of unknown sex, and 7 were subadults. For adult captures, the average initial weight was 229 ± 94 g (range = 105–480, $n = 43$), average snout–vent length was 53.0 ± 9.2 cm (range = 37–69, $n = 18$), and average total length was 64.6 ± 10.9 cm (range = 48–90, $n = 22$).

We implanted 13 snakes with radio-transmitters; however, one snake died within 1 d of release, likely of surgery-related causes. Of the other 12 radio-tagged snakes (4 males, 8 females), we recorded 374 telemetry fixes in total, with an average of 31 ± 16 telemetry fixes and 26 ± 13 unique locations per snake, and tracked the snakes for a mean of 77 ± 37 d (Table 1). We tracked five snakes until they entered hibernacula, between 22 September and 14 October.

Space Use.—For six female and four male radio-tagged snakes with sufficient numbers of locations for analysis, mean home range size was 18.6 ± 19.3 ha calculated with MCPs (Fig. 2), and 27.4 ± 29.5 ha calculated with 95% fixed kernel UDs (Fig. 3). The mean core use area was 6.0 ± 6.5 ha calculated with 50% UDs (Fig. 3). The four snakes that used some closed-canopy forest had significantly larger home ranges compared to the other six snakes ($W = 0$, $P = 0.01$; Fig. 4). Home range size did not differ significantly between males (MCP: 9.1 ± 7.3 ha) and females (MCP: 24.9 ± 22.8 ha; $W = 16$, $P = 0.48$), although females had a larger variance of home range sizes (Table 1). Home range size also did not differ significantly among years ($\chi^2 = 2.9$, $P = 0.23$).

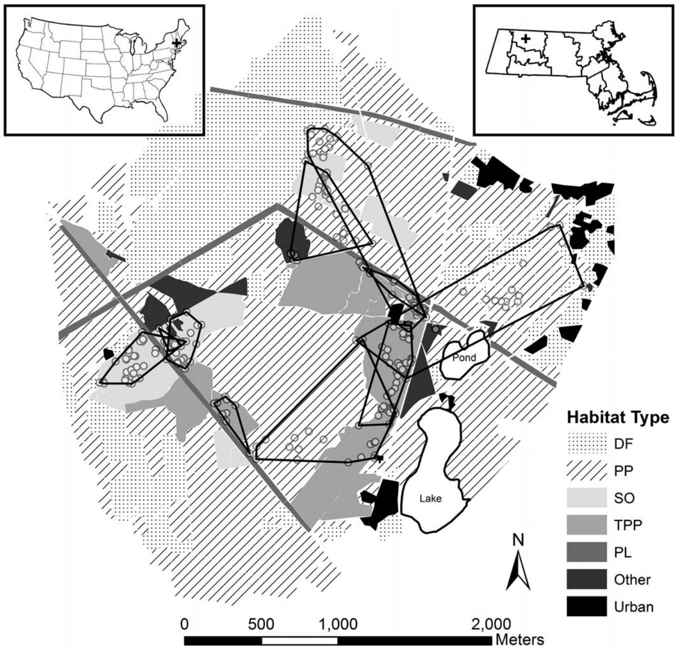

FIG. 2. The 600-ha Montague Plains study site (inset maps of location in Massachusetts, USA) with habitat type classifications (see Fig. 1 legend), telemetry fixes of 12 radio-tagged Eastern Hognose Snakes, and 100% minimum convex polygons for 10 individuals.

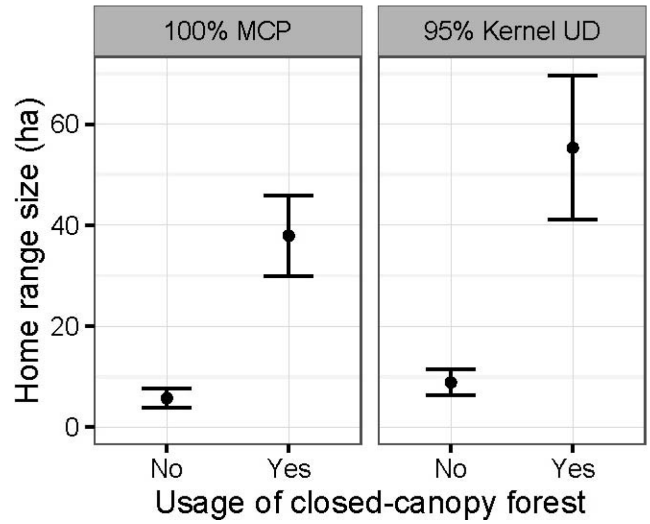

FIG. 4. Home range size (ha) computed with 100% minimum convex polygons (MCP) and 95% fixed kernel utilization distributions (UD) as a function of the observed usage of closed-canopy forest by a given snake ($n = 10$). Points and error bars represent means ± SE.

Daily movement distances ranged from 1 to 455 m/d, with a mean of 39 ± 57 m/d ($n = 298$), though the majority of movements (74%) were <50 m/d. Mean daily movement rates (averaged per snake) were similar for males (36 ± 4 m/d) and females (38 ± 33 m/d; $W = 8$, $P = 0.21$, $n = 12$), and for snakes tracked in different years ($\chi^2 = 0.1$, $P = 0.96$). Snakes that used some closed-canopy forest had higher mean daily movement rates (61 ± 17 m/d) compared to snakes that did not use closed-canopy forest (25 ± 4 m/d), but this only approached significance ($W = 5$, $P = 0.07$).

Habitat Selection.—Of 56 initial captures of snakes, most were captured in the open-canopy habitats that we extensively surveyed (Table 2). We also found an additional four snakes dead on dirt and paved roads. We observed 298 unique telemetry relocations of the radio-tagged snakes (excluding capture locations). Examining descriptive statistics, actual relocations of radio-tagged snakes were more often observed in open-canopy scrub oak and treated pitch pine habitats, and less often in closed-canopy forest and power line corridors when compared to random, available locations (Table 2). All five hibernacula sites that we observed were located in early-successional habitat (two in treated pitch pine, two in scrub oak, and one in other early-successional habitat).

The model with the lowest AIC_c value in the paired logistic regression analysis included pitch pine, deciduous forest, and power line corridor habitats, and explained 17% of the deviance

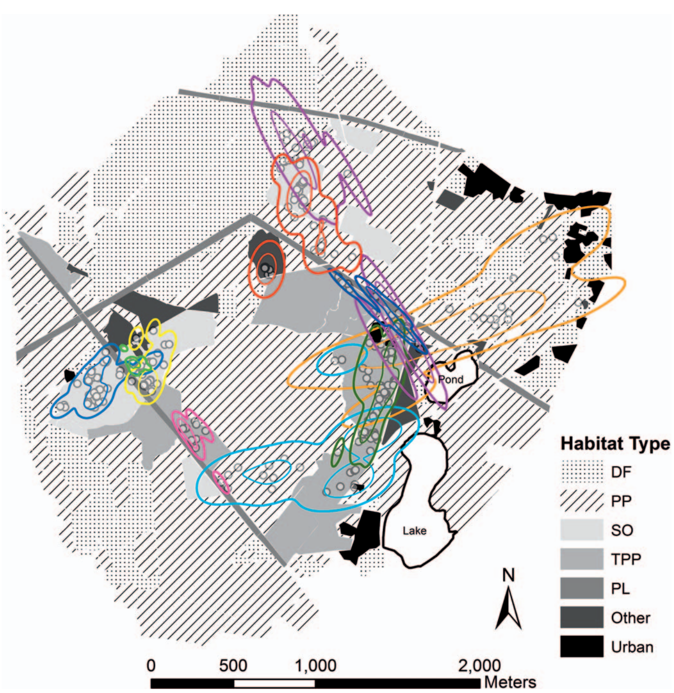

FIG. 3. Ninety-five percent and 50% fixed kernel utilization distributions (UD) for 10 Eastern Hognose Snakes, each represented by a different color. The outer, thick lines are 95% UDs and the inner, thin lines are 50% UDs.

TABLE 2. Descriptive statistics of habitat selection for Eastern Hognose Snakes, including initial capture locations, actual relocations, and random, available points in different habitat types in the study site. Percentages of locations in each habitat type are shown, with sample sizes in parentheses for actual locations. Initial capture locations include PIT-tagged snakes, whereas unique telemetry relocations only consist of unique relocations of the 12 radio-tagged snakes.

Habitat type	Initial capture locations	Unique telemetry relocations	Random, available points
Treated pitch pine	64% (36)	39.3% (117)	33.8%
Power line corridor	14% (8)	2.3% (7)	4.6%
Scrub oak	11% (6)	35.6% (106)	29.2%
Other early-successional or sand pit	4% (2)	4.7% (14)	4.9%
Closed-canopy pitch pine forest	7% (4)	13.1% (39)	21.8%
Closed-canopy deciduous forest	0% (0)	3.0% (9)	4.2%
Urban	0% (0)	2.0% (6)	1.4%

TABLE 3. The top paired logistic regression models (<7 ΔAIC_c) assessing habitat selection in Eastern Hognose Snakes by examining telemetry use relocation data and corresponding random locations as a function of habitat variables and distance to edge variables. Presented are the models, number of parameters (*K*), proportion of deviance explained (D^2), Akaike's Information Criterion value corrected for small sample sizes (AIC_c), difference in AIC_c from the top model (ΔAIC_c), and model weight (ω_i). Habitat variables were scrub oak = SO, treated pitch pine = TPP, power line corridor = PL, pitch pine forest = PP, deciduous forest = DF, other early-successional or sand pit habitat, and urban habitat. Edge variables were: road edge = road, forest/early-successional edge, lake edge, urban edge, and any edge.

Model	*K*	D^2	AIC_c	ΔAIC_c	ω_i
DF+PL+PP	3	0.174	347.405	0	0.303
DF+PL+PP+road	4	0.175	348.929	1.524	0.142
DF+PL+PP+SO	4	0.175	349.030	1.625	0.135
DF+PL+PP+TPP	4	0.174	349.325	1.920	0.116
DF+PL+PP+SO+road	5	0.177	350.403	2.998	0.068
DF+PL+PP+SO+TPP	5	0.176	350.582	3.177	0.062
DF+PL+PP+TPP+road	5	0.175	350.865	3.460	0.054
DF+PL+PP+SO+TPP+road	6	0.178	351.882	4.477	0.032
DF+PP+SO+TPP	4	0.165	353.146	5.741	0.017
DF+PP+SO+TPP+road	5	0.167	354.222	6.817	0.010

in the data (Table 3). Model-averaged results indicated that snakes significantly avoided these three habitat types, as the 95% CIs of the odds ratios of these variables were <1 (Table 4). The other predictor variables in the models had less support, because their 95% CIs of the odds ratios overlapped 1. Therefore, any additional variability of snake habitat use, independent of avoiding the above three habitat types, was not further explained by selection or avoidance of other habitat types or distance from the different edge types.

Mark and Recapture and Survival.—We recaptured two PIT-tagged snakes in different years (5% of PIT-tagged snakes, $n = 42$), with one snake caught in 2008 and recaptured in 2009, and one caught in 2009 and recaptured in 2011. Our recapture rate within years was 9% ($n = 33$, excluding snakes that we tracked with radio-transmitters).

We estimated survival for 12 radio-tagged snakes that we tracked for 915 observation days. We observed three known mortalities, two of which appeared to be the result of predation and one of an unknown cause. Our constant survival model yielded a daily survival rate of 0.9967 (95% CI = 0.9899 to 0.9989); based on this model, the probability of a snake surviving for the entire active season (150 d) was 0.61 (95% CI = 0.22 to 0.85). Survival was unrelated to the snake's sex ($\beta = 0.13$, 95% CI = −2.27 to 2.54), the usage of closed-canopy forested habitat ($\beta = 0.32$, 95% CI = −2.08 to 2.73), or the snake's initial weight ($\beta = -0.003$, 95% CI = −0.014 to 0.008), as indicated by CIs encompassing 0.

DISCUSSION

We demonstrated that Eastern Hognose Snakes avoided closed-canopy forest within our study site and instead used managed, open-canopy habitats such as scrub oak barrens and heavily thinned pitch pine. Similarly, Eastern Hognose Snakes in other populations prefer open, disturbed, xeric habitats with sandy soils, and avoid closed-canopy forested areas (Platt, 1969; Plummer and Mills, 2000; LaGory et al., 2009, Goulet et al., 2015). Other snake species associated with early-successional, disturbance-dependent habitats respond positively to fuels reduction and habitat restoration activities such as prescribed burning, mowing, and silviculture (Perry et al., 2009; Bailey et al., 2012; Howey et al., 2016). Forest management is especially important for snake species associated with disturbance-dependent ecosystems, because management helps retain these natural ecosystems and prevents competition from fire-intolerant vegetation species (Nowacki and Abrams, 2008; Waldron et al., 2008).

TABLE 4. For the variables in the top paired logistic regression models (models with $\Delta AIC_c < 7$; these models comprised >94% of the weight of the candidate model set), presented are the model-averaged parameter estimates (β), the odds ratios, the odds ratios' 95% CIs (lower and upper CI), and variable importance scores. The importance scores were calculated by summing the model weights across all models containing the variable.

Variable	β	Odds ratio	Lower CI	Upper CI	Importance
DF	−3.926	0.020	0.002	0.248	0.939
PL	−3.395	0.034	0.003	0.347	0.912
PP	−5.163	0.006	0.001	0.041	0.939
Road	−0.003	0.997	0.990	1.004	0.306
SO	0.960	2.612	0.272	25.08	0.324
TPP	0.483	1.622	0.320	8.227	0.291

The association of Eastern Hognose Snakes with open-canopy habitats could be because of thermoregulatory benefits, suitable hibernacula and nesting sites, increased food availability, and suitable cover from predators found within open-canopy habitats (Gregory et al., 1987; Plummer and Mills, 2000; Halstead et al., 2009). Our observed hibernacula were located in open-canopy, early-successional habitat, similar to Eastern Hognose Snake hibernacula in eastern Massachusetts (Buchanan, 2012). We often observed radio-tagged snakes under leaf litter, graminoids, or shrubs in open-canopy habitats, and occasionally observed snakes taking cover underground in burrows at the base of shrubs. The sandy soils of PPSO barrens permit burrowing behavior that facilitates thermoregulation, predator avoidance, and location of prey (Platt, 1969; Plummer and Mills, 2000). Given that Eastern Hognose Snakes maintain relatively high body temperatures relative to other snake species (Platt, 1969), and ambient temperatures are important to their activity (Plummer and Mills, 2010; Buchanan et al., 2016), selection of open-canopy habitats could be especially important for effective thermoregulation. Especially in northern temperate areas, the relatively warm temperatures of open-canopy habitats could facilitate efficient movement, foraging, and reproduction (Cunnington and Cebek, 2005; Peet-Paré and Blouin-Demers, 2012), as observed for other snake species at the northern edge of their ranges (Blouin-Demers and Weatherhead, 2001; Row and Blouin-Demers, 2006).

Our habitat selection analysis defined availability in relation to a snake's specific location at a given time and its likely movements (Arthur et al., 1996; Timm et al., 2014), and we paired available points with specific snake relocation points in the paired logistic regression analyses. Each radio-tagged snake was within likely movement distance to forested habitat during our study and could have selected forested habitat, but instead, the snakes mostly avoided forests and used scrub oak and treated pitch pine. Our analytical method is arguably an improvement over traditional, compositional habitat selection analyses that often are used in snake studies (e.g., LaGory et al., 2009; Bailey et al., 2012), because traditional analyses can have arbitrary boundaries for available habitat and do not take into account the likely movements of individual animals (Rhodes et al., 2005; Forester et al., 2009). We were more likely to detect snakes moving along dirt roads in the power line corridors than in less exposed habitats and therefore biases in capture rates of PIT-tagged snakes in power line corridors could have occurred, despite their empirically low use by radio-tagged snakes. Corridors appeared to have some suitable grassy and shrubby vegetation (Akresh, 2012), but other factors such as soil compaction, or the lack of relatively tall vegetation and extensive leaf litter, may have deterred snakes from using corridors more extensively (Platt, 1969; Buchanan, 2012).

Our relatively small sample sizes and use of a single study area preclude us from making broad definitive conclusions based on our results. In some analyses, the small number of snakes in our study may have limited the statistical power needed to detect significance (e.g., in differences among years and between sexes). Sample sizes also limited our ability to address monthly variation in daily movements (Buchanan et al., 2016) in our habitat selection analyses. We did not examine individual variability in our habitat selection model because of the difficulty in including random effects in paired logistic regression. Nevertheless, our significant finding that Eastern Hognose Snakes avoid unmanaged, closed-canopy forest is consistent with reports of snakes' habitat selection in other study sites (e.g., Plummer and Mills, 2000; LaGory et al., 2009); therefore, this principal result would likely still be significant with a larger sample size of radio-tagged snakes or accounting for additional variability in our analyses.

We observed a mean home range size with MCPs of 18.6 ha, smaller than mean home range sizes (using MCPs) found for Eastern Hognose Snakes in other studies throughout the species range (New Hampshire: 72.7 ha, Goulet et al. [2015] and 51.7 ha, LaGory et al. [2009]; Arkansas: 50.2 ha, Plummer and Mills [2000]; Ontario: 39.4 ha, Robson and Blouin-Demers [2013]; Massachusetts: 31.0 ha, Buchanan [2012]). Variation in sampling duration and number of telemetry locations may have contributed to some of the variation in snakes' home range size among studies. Nevertheless, the number of unique use locations or tracking duration did not affect home range size in our study; if we had restricted our home range size estimates to snakes that had at least 20 or 30 unique locations, the mean MCP size would have been relatively small (22.6 ha or 19.0 ha, respectively). Additionally, our average daily movement (39 m/d) was much smaller than that reported from Arkansas (119 m/d; Plummer and Mills, 2000), but was similar to daily movements found in eastern Massachusetts (25.9 m/d; Buchanan, 2012); this latter study also had the closest mean home range size compared to our study. Therefore, it seems likely that snakes in our study site had smaller home ranges compared to most of the other populations of Eastern Hognose Snakes (Plummer and Mills, 2000; LaGory et al., 2009; Robson and Blouin-Demers, 2013).

The relatively small home range sizes and movement rates that we observed suggest that our study site encompasses less dispersed, and higher quality, resources and habitat for Eastern Hognose Snakes than other study sites (Gregory et al., 1987; Plummer and Congdon, 1994). Indeed, the study sites with the largest observed home ranges (Plummer and Mills, 2000; LaGory et al., 2009; Goulet et al., 2015) appear to have more closed-canopy forest and smaller, more disjunct patches of open-canopy habitat (based on the aerial photos) when compared to our study site. Consistent with the comparison among studies, the four snakes with the largest MCPs in our own study incorporated some closed-canopy forested habitat within their home range. Large home range sizes for Eastern Hognose Snakes could result from movement through forest while traveling to, or from, preferred early-successional habitat (Halstead et al., 2009; Kapfer et al., 2010). We observed a few snakes to have at least some core use areas within the forest; some locations within forested habitat could have had suitable open-canopy microhabitat that we did not take into account in our broad-scale habitat classifications. Nevertheless, snakes that primarily used open-canopy areas also had smaller core use areas, again indicating that relatively high-quality habitat was located within these open-canopy areas. Relatively large home range size and long-distance movements could bring snakes into high levels of contact with roads or predators, thereby increasing mortality (Plummer and Mills, 2000; Fahrig and Rytwinski, 2009; Rouse et al., 2011); however, we did not observe relatively low survival in snakes that used some closed-canopy forest and had the largest home ranges.

Our seasonal survivorship estimate was within the range reported for Eastern Hognose Snakes in other studies (Parker and Plummer, 1987; Plummer and Mills, 2000; Rouse et al., 2011; Buchanan, 2012; Goulet et al., 2015), although our data may have been biased because of the small sample size of radio-tagged snakes as well as our assumption that "lost" snakes survived. Nonetheless, based on our limited data set and our model assumptions, adult Eastern Hognose Snakes in our managed study area appear to have similar survival rates compared to Eastern Hognose Snakes studied at sites that were not specifically managed for fuels reduction and habitat restoration (e.g., Plummer and Mills, 2000). Consistent with other studies of Eastern Hognose Snakes (Plummer and Mills, 2006; Rouse et al., 2011; Buchanan, 2012), we observed some road mortality, but none in our radio-tagged individuals. The impact of road mortality on Eastern Hognose Snake populations is likely to vary by site depending on the open-canopy habitat configuration in relation to roads, road abundance, and traffic levels (Rouse et al., 2011). Despite somewhat low adult survival rates and some road mortality, populations in our site and other study sites could perhaps be maintained by the relatively early maturation and high fecundity rates typical of Eastern Hognose Snakes (Platt, 1969; Plummer and Mills, 2000).

Conservation and Management Implications.—Forest management that reduces the amount of closed-canopy forest, such as with heavy thinning, should increase the amount of suitable habitat available for Eastern Hognose Snake populations. Providing large, connected areas of open-canopy habitat could be beneficial to snakes by providing adequate resources and reducing snakes' home range size. Our limited observations as well as accounts in the literature suggest roads could pose a risk to snakes, and managers should consider closing off roads in areas where priority snake populations exist. Our study adds to the growing literature that fuels reduction and habitat restoration in PPSO barrens and other disturbance-dependent ecosystems are beneficial to a wide variety of threatened wildlife reliant on these ecological communities (Wagner et al., 2003; Bried et al., 2014; Akresh and King, 2016).

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