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Spatial Ecology of the Eastern Hog-nosed Snake (*Heterodon platirhinos*) at the Northeastern Limit of its Range

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***Abstract.*—Populations at the edge of the natural range of a species may deal with ecological challenges that differ from those at the core of the range. These differences can result in different patterns of resource use, which may confound resource managers and conservation biologists who must develop management strategies based upon the best available information. One such species is the Eastern Hog-nosed Snake (*Heterodon platirhinos*), a species of conservation concern in the northeastern part of its geographic range due to habitat loss, declines in amphibian prey species, and wanton killing. To address these knowledge gaps, we used radio-telemetry to study the spatial ecology and natural history of six *H. platirhinos* at the northern-most portion of the range of the species in New York. Snakes that we tracked had mean home-range sizes (100% minimum convex polygon = 23.7 ± 21.2 ha) smaller than populations reported in New Hampshire, Massachusetts, Arkansas, and Ontario. Snakes also used forests extensively, although compositional analysis revealed that they selected open and edge habitats in greater proportion to their availability, consistent with other studies. Snakes were more likely to be found in close proximity to coarse woody debris than was randomly available, and they selected microhabitats with denser vegetation than average, but we found no evidence of selection for ground cover, canopy cover, or proximity to trees.**

Key Words.—compositional analysis; conservation; habitat selection; home-range; New York; radio-telemetry; reproduction

Introduction

Populations near the edge of the range of the species often deal with limiting factors that differ in comparison to populations in the core of the range, including changes in predation pressure (Vaupel and Matthies 2012), food availability (Ferguson and McLoughlin 2000), temperature (Sanford et al. 2006), growing season (Normand et al. 2009), and of increasing concern, climate (Opdam and Wascher 2003; Böhning-Gaese and Lemoine 2004; Moritz et al. 2008; Rodhouse et al. 2010). Conservation biologists and wildlife managers require the best natural history and ecology data to make informed decisions, but variation in limiting factors and differential response to them are often poorly documented, complicating the decision making process (Dayton 2003; Greene 2005; Bury 2006).

Heterodon platirhinos (Eastern Hog-nosed Snake) ranges across the eastern U.S. from New Hampshire to peninsular Florida, and west to central Texas and Minnesota; it also occurs in southwestern Ontario, Canada (Conant and Collins 1998). Populations of *H. platirhinos* are apparently stable across its large geographic range (Hammerson, G.A. 2007. *Heterodon platirhinos*. IUCN Red List of Threatened Species. Available at: http://www.iucnredlist.org/details/63820/0. [Accessed 20 June 2014]), but the species is in need of conservation action in the northeastern portion of its range (Therres 1999; Northeast Partners in Amphibian and Reptile Conservation [NEPARC] 2010), with local populations entirely extirpated or otherwise threatened by habitat loss, amphibian declines (its primary prey), road mortality, and direct persecution by humans (Gibbs et al. 2007; Seburn 2009; Robson and Blouin-Demers 2013). Both the Northeast Endangered Species and Wildlife Diversity Technical Committee (Therres 1999) and NEPARC (2010) list *H. platirhinos* as a species of regional concern, and it is a listed species in Connecticut, Rhode Island, New Hampshire, New York, USA, and Ontario, Canada. However, declines in snake populations receive less attention compared to more charismatic organisms, such as turtles and frogs (Meylan and Ehrenfeld 2000; Norris 2007), and snakes like *H. platirhinos* remain poorly studied. This lack of species-specific information can prevent the development of effective conservation strategies (Dorcas and Willson 2009).

Like with most snake species, little is known about the ecology of *H. platirhinos*. Indeed, as with field ecology in general, snake ecology is severely limited by a lack of replication in field studies within and among species (Belovsky et al. 2004; Mullin and Siegel 2009), and this confounds the ability to make sound conservation decisions. The few published studies suggest smaller home ranges in the northeastern past of range (New Hampshire and Massachusetts in the USA, and Ontario, Canada) than in the core of the geographic range (Plummer and Mills 2000; Lagory et al. 2009; Robson 2011; Buchanan 2012). Habitat selection has been studied even less extensively, and with less methodological replication. In New Hampshire, *H. platirhinos* select early successional, edge, and coniferous forest habitats (Lagory et al. 2009; Goulet et al. 2015), but select sand barrens and human-altered (e.g., habitat tree plantations, residential yards, and the edges of agricultural fields) in Ontario (Robson 2011). These studies suggest that resource use by *H. platirhinos* is quite variable across its wide geographic range. A better understanding of the spatial ecology and resource use by *H. platirhinos* has direct conservation value for the species, especially in the northeastern portion of its range where the species appears to be declining and yet remains poorly studied.

To address the dearth of ecological information on this regionally imperiled species, we conducted a radio-telemetry study of *H. platirhinos* to evaluate home ranges and habitat selection in a population near the northeastern edge of the range of the species. Nothing is known of the phylogeography of *H. platirhinos*, so we based our hypotheses on home range and resource selection values reported by Lagory et al. (2009) and Goulet et al. (2015), the closest population (New Hampshire) with reported spatial ecology data. We hypothesized that the natural history of *H. platirhinos* at our study site would be the same as sites in New Hampshire. We predict that the size of home ranges would be about 50 ha, and that snakes would select early successional/edge habitats. We also predict that *H. platirhinos* would show a preference for microhabitats with structural complexity, as they do in Ontario (Robson 2011) and New Hampshire (Goulet et al. 2015).

Materials and Methods

Study site—We studied *H. platirhinos* at Moreau Lake State Park (MLSP), a 1,600 ha park located in Saratoga County, New York, USA (Fig. 1). Northern portions of the park are less accessible to visitors, but the southern part has visitor amenities including camping areas, hiking trails, a nature center, and a lakefront beach, and is bordered by paved roads to the north, west, and south, and surrounded by private property. We included only the southern half of the park in this study, which is composed of a variety of natural communities. The study site was dominated by low-lying Appalachian-Oak Pine Forest (AOPF) surrounding three Eutrophic Dimictic Lakes known as Mud Pond, Back Pond, and Moreau Lake, with large patches of Beech-Maple Mesic Forest (BMMF) and Hemlock-Northern Hardwood Forest (HNHF) on the western slope, as defined by available GIS overlays of the park (Fig. 1). There were two patches of forest on the western slope that were not included in available GIS overlays, but were likely a combination of AOPF, BMMF, and HNHF based on ground truth surveys, the surrounding habitat types, and reference to Edinger et al. (2014). There is a small amount of old field habitat at the southeastern edge of the park (hereafter Open), as well as several utility right-of-ways created for power lines, similar in composition to old field habitat. Elevation in the southern portion of the park is typically 120 m, but ranges to 365 m at the peak of a long ridge that runs along the western portion of the study area.

Field and telemetry methods.—We located snakes by actively searching available habitat during the day. Search efforts were concentrated near day-use areas of the park frequented by visitors, with particular focus placed upon stereotypical *H. platirhinos* habitat (e.g., edge, early successional old field, open areas). We also encountered new snakes while tracking previously implanted snakes, particularly during the breeding season. Park staff and visitors did not report any encounters of *H. platirhinos* during the field season, despite park visitor-outreach efforts and active searching by several volunteers. Daily road-cruising by us for live or road-killed *H. platirhinos* also produced no animals (although we observed turtles, mammals, birds, and amphibians on the road). The six wire-mesh funnel traps that we set for 15 d in late April also produced no *H. platirhinos*, although they did capture several American Toads (*Anaxyrus americanus*) and a single Eastern Garter Snake (*Thamnophis sirtalis*).

We determined the sex by probing and/or tail inspection of all snakes we captured. We weighed each snake to the nearest 1 g using an electronic scale and/or spring scales and we photographed snakes next to a ruler to record snout-vent and tail length for measurement to the nearest 1 mm using ImageJ (Schneider et al. 2012). We also marked snakes using a unique scale-clip identity following a modified version of the Brown and Parker (1976) protocol. Snakes > 100 g that we captured before 1 August 2012 were surgically implanted with a 5g SB-2 radio transmitter (Holohil Systems Ltd., Carp, Ontario, Canada) by an experienced veterinarian at the Greenfield Animal Hospital (Greenfield Center, New York, USA) following the procedure described in Reinert and Cundall (1982). After surgery, we administered a course of antibiotics (Enrofloxacin) and painkillers (Meloxicam) to snakes at doses based on body weight

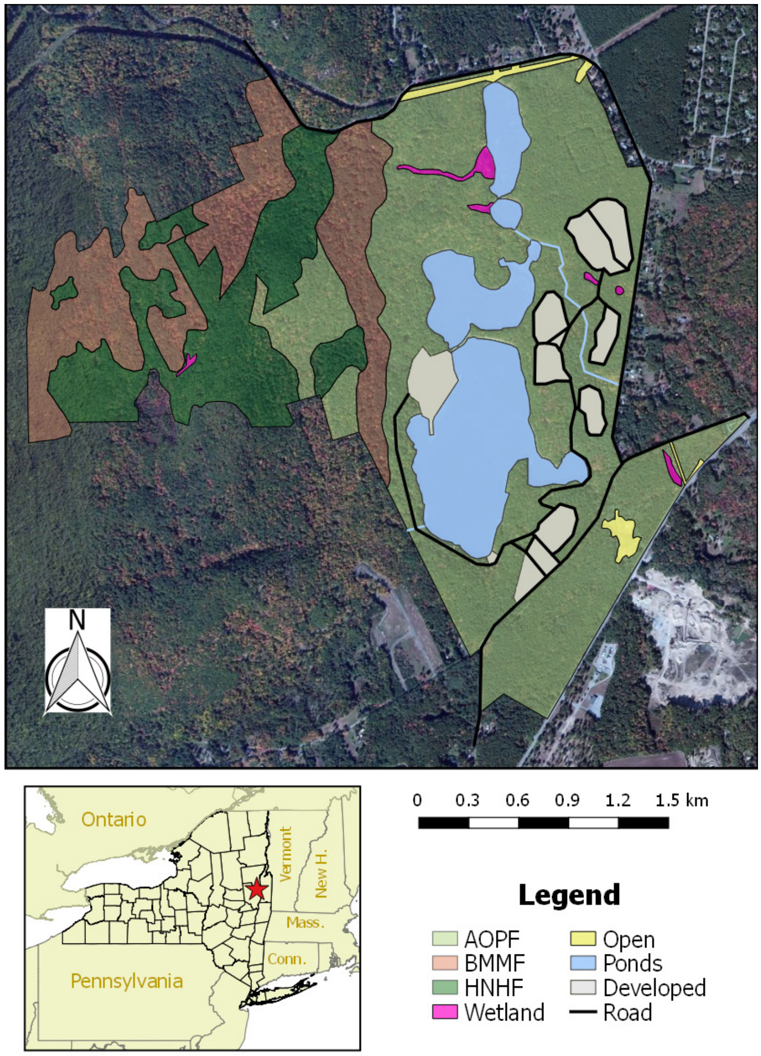

Figure 1. Geographic location of the study site, and habitat types used for habitat selection of Eastern Hog-nosed Snakes (*Heterodon platirhinos*) in this study. Hemlock-Northern Hardwood Forest (HNHF), Beech-Maple Mesic Forest (BMMF), and Appalachian-Oak Pine Forest (AOPF) were aggregated into the Forest category for analysis, but shown here to display the spatial configuration of habitat types at the study site.

and determined by the veterinarian. We held snakes in captivity prior to implantation for 1 h to 15 d depending veterinarian availability, and for recovery for 2–4 d after surgery (depending on weather conditions) until release at the original point of capture.

We located snakes using an R-1000 Telemetry Receiver (Communications Specialists Inc., Orange, California, USA) and a directional 3-element Yagi antenna every 2.3 d (± 1.7 d) from the date of release until 30 August, and then sporadically thereafter. We attempted visual contact for each relocation, but we stopped our approach when the snake reacted to our presence (e.g., snakes basking or resting coiled often tilted their head and increased tongue-flicking upon noticing the observer). Snakes were handled only during initial capture and processing, with very occasional and opportunistic outreach with park staff and visitors (≤ 2 times per snake; not every snake was used for outreach). We recorded habitat and behavioral information for every snake telemetry relocation. We also recorded time and GPS location using a handheld GPS unit and recorded snake visibility (concealed, partially concealed, fully visible), percentage canopy cover (visual estimation to the nearest 25%), percentage ground cover (visual estimation of bare substrate visible to the nearest 25%), presence of coarse woody debris (CWD; downed logs >10 cm in diameter or large branchy debris piles), distance (m) to nearest overstory tree (diameter at breast height > 10 cm), vegetative cover (estimated into sparse, medium, and dense categories), and snake reaction to human observer (before handling). Using a random number generator, we compared ground

Table 1. Size, sex, number of locations, and home range estimates (100% minimum convex polygon [MCP] and kernel density estimator [KDE], in ha) for all Eastern Hog-nosed Snakes (*Heterodon platirhinos*) radio-tracked in 2012. Last date of telemetry for all snakes was 5 January 2013.

ID (sex)	Mass (g)	Start Date	Locations	MCP (ha)	95% KD (ha)	50% KD (ha)
1 (M)	157	29 May	49	12.2	19.8	5.60
2 (F)	423	5 June	33	4.70	12.8	3.70
3 (M)	214	8 June	44	9.50	36.0	9.60
4 (F)	618	8 June	44	19.1	53.6	14.0
5 (F)	640	8 June	40	52.5	150.6	36.7
7 (F)	120	28 June	18	1.30	3.10	0.70

cover, canopy cover, distance to nearest tree, vegetative cover, and presence of CWD to random sites within 15 m of the relocation site. We selected these microhabitat metrics based on the natural history literature and ecological studies of *H. platirhinos* and other snakes, but also those that are easily measured by land managers. The majority of the study site consisted of loamy sand (www.websoilsurvey.sc.egov.usda.gov), and we did not attempt to quantify selection based on this metric.

Statistical analyses.—We analyzed habitat data and snake locations using the Geospatial Modeling Environment (Beyer, H. L. 2012. Geospatial Modelling Environment, Version 0.7.2. Available at: www.spatialecology.com/gme. [Accessed 1 June 2014]) in ArcGIS 10.1. For each snake, we estimated home range by calculating the 100% minimum convex polygon (MCP), and 95% and 50% kernel density estimates (KDEs; Worton 1989). For KDEs, we attempted the least-squares cross validation method but the algorithm did not converge for all snakes, so we used the reference bandwith, as per Seaman and Powell (1996). We modified MCPs and KDEs by removing open water area from home ranges when appropriate, as snakes were never seen nor suspected to have entered water. The minimum number of relocations needed for MCP and KDEs was determined to be 15 for *H. platirhinos* in New Hampshire (Lagory et al. 2009), and we exceeded this number for each snake (Table 1). To calculate distance between relocation, we divided the sum of distance between successive telemetry locations by the total number of relocations for each snake.

We used compositional analysis (Aebischer et al. 1993) to determine whether patterns of habitat usage by snakes differed from the habitat actually available at the study site. Our compositional analysis used Resource Selection 8.1 (Leban, F. A. 1999. Resource Selection 446, Version 8.1. University of Idaho. Available at: www.msu.edu/course/fw/424/Fred%20Leban/Resource%20Selection. [Accessed 19 June 2014]) to analyze spatially-explicit values derived from ArcGIS 10.1. We aggregated the natural communities of the park (Fig. 1) into four broad habitat categories that we think would be perceived as substantially different to snakes: forest types (AOPF, BMMF, and HNHF), wetland types (any swamp or riparian area), open areas (old field, utility right-of-ways, etc.), and developed/altered areas (paved roads, campsites, buildings, parking lots, and other high-use areas). We also created an edge category (15 m buffer where forest was adjacent to open, developed, or large open body of water) based on high use of edge habitat as reported in Lagory et al. (2009). To determine habitat availability, we buffered all relocations for each snake by a radius equal to that of the maximum distance between two relocations of an individual divided by the number of days between relocations. The area within these buffers was considered available to that snake, as it represented the locations the individual could have reached based on its observed movement habits. We also removed any open-water area from habitat analyses. We compared ground cover, canopy cover, vegetative cover, and presence of CWD to random sites using Chi-Square and compared distance to nearest tree using a Student's *t*-test. For both tests, $\alpha = 0.05$.

Results

Drift fence captures.—We captured 12 *H. platirhinos* individuals in all age classes, including neonates, juveniles, and reproductive adults. Most snakes ($n = 10$) were initially located in the northeastern portion of the study area. We collected telemetry data from six sexually mature snakes (two males and four females), with the number of relocations per animal ranging from 18 to 49 (mean = 38) based on the date of original capture, weather, and accessibility (Table 1). As of 6 October 2013, we confirmed visually that all but two *H. platirhinos* were alive, with the remaining two snakes presumed to be alive underground. For these two snakes, we tracked transmitter signals to areas of bare soil (suggesting they were underground) and there was no evidence of depredation. The final relocations on 5 January 2013 also suggested that each snake was underground, as each location was near (< 60 m) the previous location in October, and we did not find transmitters above ground. We observed three telemetered snakes (1, 3, and 4) above ground the following spring: two due to unexpectedly long transmitter battery life and one was

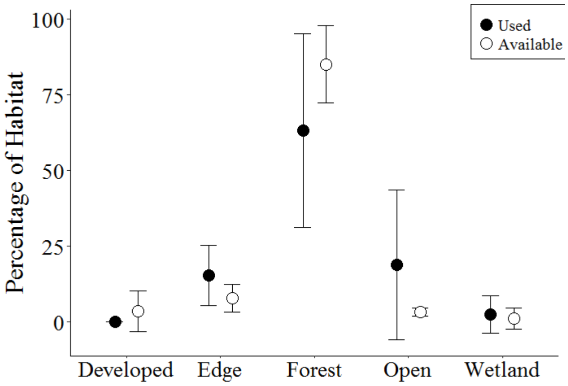

Figure 2. Mean proportional distribution (+1 SD) of habitats used by and available to all Eastern Hog-nosed Snakes (*Heterodon platirhinos*) during the study period. Used proportion refers to number of relocations, available proportion to area coverage.

Table 2. Comparative use of habitats by Eastern Hog-nosed Snakes (*Heterodon platirhinos*) determined by compositional analysis. Signs (+ or -) represent greater or lesser use of that row habitat relative to column habitat, e.g., edge is used at a greater rate than developed; triple signs indicate significant difference at $P \leq 0.050$. Rankings are ordered from 0–4 (least to most use) based on availability.

	Forest	Open	Edge	Wetland	Developed	Rank
Forest		-	-	+	+	2
Open	+		-	+	+++	3
Edge	+	+		+	+++	4
Wetland	-	-	-		+	1
Developed	-	-	-	-		0

observed incidentally by the park educator (Vanek et al. 2014). We did not monitor hibernacula in the spring for logistic reasons.

Home range.—We calculated home range estimates for the six adults captured before 1 August 2012 (Table 1). Minimum convex polygons were 1.3–66.9 ha, with a mean of 23.7 ± 21.2 ha. Home ranges overlapped substantially, with the exception of Snake 2, which was captured in an area apart from other study animals. Ninety-five percent KDEs had a larger area than MCP estimates, with calculated values from 3.1–150.6 ha and a mean of 49.3 ± 54.3 ha. Core home range (50% KDEs) estimates ranged from 0.7 to 36.8 ± 13.1 ha (Table 1). Removing the area of the lake from MCPs decreased average home range size by 18.4%, but only reduced 95% KDEs by 6.7%, and 50% KDEs by 2.3%. Average daily movement for snakes (estimated by the distance between successive relocations divided by the days between relocations; Table 1) was 36.7 ± 4.8 m. Mean straight-line distance between hibernacula was 638.5 ± 877.1 m, and Snakes 1 and 7, a male-female pair that were observed together multiple times during the late summer breeding season (n = 9), did not hibernate together (325 m apart). *Heterodon platirhinos* at MSLP regularly crossed unpaved hiking trails (John Vanek, pers. obs.) but were never seen to have crossed paved roads, nor were they recorded on opposite sides of paved roads, although they were occasionally (n = 11) found in close proximity (< 10 m) to paved roads.

Habitat selection.—*Heterodon platirhinos* at MLSP made extensive use of forest (61.8%, n = 141 locations), and more specifically AOPF, which was the most common habitat type available (> 212 ha and roughly 47% of the study site; Fig. 1). Most initial snake locations (seven of 12) and subsequent telemetry relocations (51.3%; n = 117) were within AOPF. The second most common habitat type used by telemetered snakes was open (18.9%, n = 43), followed by edge (17.1%, n = 39). The remaining relocations occurred in wetlands (Snake 2 only, n = 5). Snake 5 was the only snake to use HNHF (n = 22) and BMHF (n = 2). We did not locate any snakes in developed areas, but snakes were occasionally near them.

Using aggregated forest types, snakes used habitats non-randomly relative to availability ($\lambda = 0.181$, $\chi^2 = 10.25$, df = 4, $P < 0.050$). *Heterodon platirhinos* selected open habitat (featuring sandy soil and low canopy cover) compared to other habitat types. Selection for this open habitat was greater than all other habitat types and developed habitat was completely avoided (Table 2). Snakes were more likely to be found near CWD ($\chi^2 = 0.035$, df = 1, $P < 0.001$) compared to random sites, and more likely to be found in areas of higher vegetative cover compared to random sites ($\chi^2 = 14.42$, df = 2, $P < 0.001$; Fig. 2). There was no difference in snake locations and random sites for ground cover ($\chi^2 = 16.16$, df = 1, $P = 0.852$), distance to nearest tree ($t = 1.20$, df = 8, $P = 0.131$), or canopy cover ($\chi^2 = 2.95$, df = 1, $P = 0.086$).

All snakes were still active and above ground in mid-September, and four of six telemetered snakes were still active in October. By 5 January 2013, all snakes were underground with active telemetry signals, and Snakes 2 and 7 had not detectably moved since October. *Heterodon platirhinos* that we tracked at MSLP overwintered in a variety of habitat types, including AOPF, open, and BMMF. The majority of *H. platirhinos* did not hibernate near the location of capture, with the exception of Snake 3 and 7, both of which hibernated approximately 30 m of their initial capture locations. In addition, the initial location of Snake 3 was 10 m from of an April 2013 observation. Hibernacula for Snakes 1, 3, 4, 5, and 7 were located in areas of tree roots and/or rodent burrows, but Snake 2 ostensibly dug a hibernaculum in bare soil.

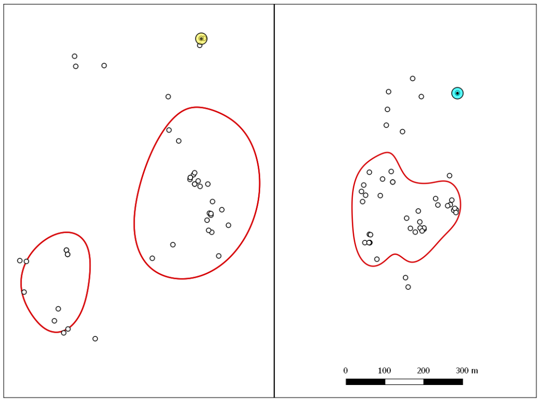

Figure 3. Telemetry locations (white circles) and 50% KDE (red polygons) for Snake 1 (left) and Snake 4 (right). The 50% KDE of Snake 1 excludes its hibernaculum (blue circle) and the 50% KDE of Snake 4 excludes the location of a nest that resulted in 37 neonates.

Discussion

Home range.—We calculated both MCP and kernel density home range estimates to facilitate comparison with other studies, but we interpret KDEs with caution, given their tendency to overestimate home range size at moderate sample sizes (Row and Blouin-Demers 2006). Indeed, 95% KDEs were consistently much larger than MCP estimates for all individuals, and we suggest MCP is a more useful estimate for the current study. In addition, 50% KDs, which are often used to describe the core of a home range, did not include the hibernacula for Snake 1 or 2, and did not include the nest for Snake 4 (Fig. 3). Row and Blouin-Demers (2006) suggest manually adjusting smoothing factor (h) of kernels until the 95% KDE is approximately equal in size to the 100% MCP, and then developing core home ranges from this adjusted KDE. However, our calculated core home ranges were based on the 95% KDEs, which were larger than MCPs. Therefore, recalculated core home ranges would be smaller, and therefore still not include hibernacula or nest sites. Alternatively, MCPs can include areas not actually used by an animal, and are highly dependent on sample size (Burgman and Fox 2003). The lack of telemetry relocations during September and October may explain why KDEs did not include hibernacula, but do not explain the exclusion of the nest of Snake 4. When possible, telemetry effort should be evenly distributed throughout the activity period of a species. However, this is not always feasible, and therefore we suggest that MCPs are a more accurate home range estimate for *H. platirhinos* at MLSP and should be given more weight in management decisions over KDEs.

The average MCP home range (23.7 ha ± 21.2) was low compared to other studies of *H. platirhinos*, even if we did not remove the lake area from MCP estimates. However, we acknowledge that this is may be a function of the small number of snakes tracked. Lagory et al. (2009) reported an average MCP of 51.7 ± 14.7 ha, Robson (2011) reported 39.43 ± 6.3 ha, and Plummer and Mills (2000) reported 50.2 ± 6.4 ha, but Buchanan (2012) reported a similar MCP of 31.0 ± 15.6 ha. A subsequent study of home range at the same site as Lagory et al. (2009) revealed an even larger home range of 72.7 ± 35.3 ha (n = 5). Although home range size is usually thought to increase with the number of relocations, in organisms with temporal peaks in activity, such as *H. platirhinos* (Gibbons and Semlitsch 1987), home range size is likely better estimated by relocations over a relatively long tracking period. For example, the home range estimates of Snakes 1–5 before 13 July (when Snake 7 was captured) were 36.7% ± 12.7 of their eventual size. However, removing the small home range of Snake 7 only increased mean MCP size to 26.2 ± 9.9 ha, although it did reduce the standard deviation. In addition, only one of the six snakes tracked had a home range comparable to the approximately 50 ha average of snakes in Arkansas and New Hampshire, and this is much smaller than the > 200 ha maximum of a single snake in Massachusetts (Buchanan 2012), so the small homes ranges at MLSP do not appear to be strongly influenced by the small number of snakes tracked.

Alternatively, Gibbons and Semlitsch (1987) found that *H. platirhinos* in South Carolina had activity peaks in May and October, both of which were not included in tracking periods in this study, which may have resulted in smaller calculated home range sizes. However, as MLSP is approximately 1,400 km north of the South Carolina site, spring activity was likely delayed, and fall activity was likely early, as the average distance from the single mid-October relocation to hibernacula was only 19.8 ± 15.3 m, compared to a late August mean distance of 301.9 ± 216.6 m. Indeed, the average May 2012 temperature at the South Carolina site was 7° C warmer than MLSP, and over 9° C warmer that October (www.wunderground.com). Once snakes were underground for the winter, it was difficult to confirm their precise location, so hibernacula would be best identified during emergence the following spring. However, logistics, including transmitter battery life limitations, prevented spring emergence monitoring.

The reason behind the disparity in home range sizes between populations is unclear, but could be due to differences in prey availability, winter hibernacula, or nesting habitat, all of which are consistent of species living at the edge of their range. We do not think occasional outreach handling impacted snake movements or home range. For example, Snake 7 was observed to catch and consume a wild *A. americanus* minutes after being tracked, handled, and released, only 2 m from us (John Vanek, pers. obs.). Finally, the wide inter-individual variation is common in radio-telemetry of this species, and may be related to the body size variation among the sampled snakes. Future studies should address the impact of snake size and sex on home range size.

Habitat selection.—*Heterodon platirhinos* in the park used forested areas that constituted the majority of the area, but also demonstrated strong selection of open habitats relative to their availability, which is consistent with other published studies and natural history observations (Platt 1969; Plummer and Mills 2000; Lagory et al. 2009; but see Robson 2011). Goulet et al. (2015) describe habitat selection at the home range scale of snakes from the same study area as Lagory et al. (2009), and showed non-random selection for Hemlock (*Tsuga canadensis*) and pine (*Pinus* sp.) stands, in contrast to the results of Lagory et al. (2009). Although we did not have the statistical power to examine habitat selection of different forest types, our observations of extensive forest use, although not selection, are consistent with their results of selection towards forests.

With the exception of Snake 3, a male that remained in open habitat during much of the field season, females left open habitat and generally returned to forests within a day of nesting. Nesting was confirmed for Snake 4 (Vanek and Wasko 2014), and strongly suspected for Snakes 2 and 5 based on behavior and subsequent declines in body mass. So, while *H. platirhinos* at MLSP spent the majority of their time in forests and may use them successfully for foraging and other needs, females still require access to areas with sandy soil for successful nest excavation and successful incubation (Cunnington and Cebek 2005). At MLSP and much of the surrounding area, these areas are small, patchy, and regularly used by pedestrians, vehicles, and heavy machinery. In regions with predominantly heavy or compact soils, local populations may largely be limited by access to isolated, protected nesting habitat.

Similarly, habitat fragmentation by even small paved roads may represent a barrier to dispersal. Although *H. platirhinos* were never found to have crossed paved roads based on analysis of radio-telemetry data, snakes 4 and 5 were initially captured under the guardrail of the road at the northern border of the park, < 1 m from the pavement. Snake 2 was occasionally located in the ditch on the side of the road to at the southern border. In 2006 a female was found road-killed (Kenneth Barnett, pers. comm.) a few meters from where Snakes 4 and 5 were initially located. This is consistent with recent work indicating that *H. platirhinos* avoids paved roads (Plummer and Mills 2006; Robson and Blouin-Demers 2013). Habitat fragmentation has been offered as a hypothesis for regional *H. platirhinos* decline (Gibbs et al. 2007), and the increasing encroachment of roads into natural areas may isolate sub-populations, likely restrict gene flow, limit access to mates, or prevent movement between nest sites and hibernaculum. Alternatively, artificially maintained open areas may provide crucial nesting habitat in areas where natural disturbances are prevented by human intervention. We believe this possibility should be investigated further.

Unlike other regional species known to hibernate communally (e.g., Eastern Ratsnake, *Pantherophis alleghaniensis*, North American Racer, *Coluber constrictor*, and Timber Rattlesnake, *Crotalus horridus*; Gibbs et al. 2007), we found no evidence of communal denning, although it is possible that non-tracked snakes shared hibernacula with telemetered snakes. *Heterodon platirhinos* on barrier islands in southern New York are known to communally hibernate (John Vanek, pers. obs.), suggesting that hibernacula at MLSP are not limiting. This is unsurprising given that *H. platirhinos* is thought to use a wide range of hibernacula, such as rodent burrows or rock crevices, but also able to excavate their own dens in sandy soil (Ernst and Ernst 2003; Gibbs et al. 2007, John Vanek, pers. obs.). These potential hibernacula are likely to be scattered and widely available. Though we captured Snakes 3, 4, and 5 on the same day in close proximity to each other (and possibly to hibernacula), these individuals hibernated separately and hundreds of meters from their initial capture location). Fidelity to hibernacula is known in some populations of *H. platirhinos* (John Vanek, pers. obs), so the close proximity of the three individuals despite their use of divergent hibernacula the following winter may suggest plasticity in winter hibernation locations.

Heterodon platirhinos was not found to preferentially use areas of bare soils or open canopy in comparison to random sites, despite selecting for open habitat. This selection is likely a result of the small area of open habitat available, as random sites were often located in adjacent forest/edge habitat when snakes were using open areas. The high use of medium and dense vegetation and proximity to CWD compared to random sites should be taken into consideration when assessing habitat, as it likely provides protection from predators, thermoregulatory options, and habitat for anuran prey. This is consistent with other studies showing high use of structurally complex habitat types (Robson 2011; Buchanan 2012; Goulet et al. 2015), and underscores the importance yet difficulty of incorporating probability of detection into surveys for reptiles, especially snakes (Mazerolle et al. 2007; Steen 2010).

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