The Journal of Wildlife Management 85(5):838–846; 2021; DOI: 10.1002/jwmg.22049

Featured Article

Eastern Hog-Nosed Snake Habitat Selection at Multiple Spatial Scales in Ontario, Canada

LAURA E. ROBSON,[1] *Department of Biology, University of Ottawa, 30 Marie-Curie, Ottawa, ON K1N 6N5, Canada*
GABRIEL BLOUIN-DEMERS,[2] *Department of Biology, University of Ottawa, 30 Marie-Curie, Ottawa, ON K1N 6N5, Canada*

ABSTRACT Habitat loss is the greatest contributor to the decline of species globally. To prioritize protection of imperiled species, it is important to examine habitat use at multiple spatial scales because the availability of different resources and habitat features is scale dependent. We conducted a radio-telemetry study in the Long Point region of Ontario, Canada, in 2009 and 2010 to examine habitat selection at multiple spatial scales by eastern hog-nosed snakes (*Heterodon platirhinos*), a species at risk in Canada. We documented the habitat composition of home ranges compared to the surrounding landscape, the selection of locations within home ranges based on classified satellite imagery, and the use of microhabitat features based on site characterization in the field. At the scale of the home ranges, hog-nosed snakes avoided areas of agriculture and selected sand barrens. Within home ranges, hog-nosed snakes selectively used areas altered by humans (e.g., residential sites, openings in tree plantations). Microhabitats used by hog-nosed snakes had more woody debris, logs, and lower vegetative coverage than adjoining random sites. Because hog-nosed snakes prefer open areas and require sandy soils for nesting, management efforts should focus on the conservation and maintenance of sand barrens and patches of early successional forest.

KEY WORDS eastern hog-nosed snake, habitat selection, *Heterodon platirhinos*, Long Point, multiple spatial scales, nesting, reptile conservation.

At the global scale, habitat destruction is the leading cause of species decline and extinction (Taylor et al. 2011, Tilman et al. 2017). Different animals have different habitat needs; however, what is common among all species is that when resources are reduced or the condition of habitat degrades, viable populations cannot be sustained (Hanski 2005, Carvajal et al. 2018). This is especially true of species that are not quick to adapt to human-altered environments. For instance, high extinction rates were documented and forecasted for lizards unable to track their changing thermal environment (Sinervo et al. 2010). In a changing environment where land is converted to agriculture or where urban development occurs, it becomes increasingly important to purposely save wild spaces for wildlife. Fragments of forest or other native vegetation, left after development, may leave insufficient space and resources for viable populations to persist (Fahrig 2003, Hanski 2005). Reptiles face unique conservation challenges because they are not as mobile as mammals and birds. Thus, industrial and urban developments that fragment a landscape into isolated patches can be particularly detrimental to reptile populations (Fahrig 2003, Schneider-Maunoury et al. 2016). Accordingly, >20% of reptile species worldwide are threatened with extinction (Böhm et al. 2013, International Union for the Conservation of Nature 2020). The situation of reptiles is especially dire in Canada where the ranges of most species overlap the most densely populated and urbanized southern regions (Mullin and Seigel 2009, Lesbarrères et al. 2014). In these areas, habitat is fragmented and reptiles face additional pressures from infrastructure such as roads (Row et al. 2007, Robson and Blouin-Demers 2013, Proulx et al. 2014). Reptiles are proportionally the most at-risk group of animals in Canada (Species at Risk Act 2019). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) lists 22 of 25 (88%) snake species it has assessed as at-risk. The protection of species at risk largely depends on reliable scientific information so that appropriate recovery and conservation plans may be developed (Gardiner et al. 2013), but in the case of reptiles, basic life-history information, particularly for Canadian populations, is often lacking because they lead cryptic lives and are difficult to study (LaGory et al. 2009, Mullin and Seigel 2009, Lesbarrères et al. 2014).

Habitat selection can occur at multiple spatial scales (Owen 1972, Johnson 1980); thus, researchers attempting to define habitat selection of species should include several levels. According to Johnson (1980), first-order habitat selection defines the geographic range of the species, second-order habitat selection describes home-range selection within that larger landscape, and third-order habitat selection establishes which specific habitat components individuals use within their home ranges. By dividing habitat

Received: 19 August 2020; Accepted: 24 February 2021

[1] *E-mail: lrobson84@gmail.com*
[2] *Current affiliation: Science Department, Shawnigan Lake School, 1975 Renfrew Road, Shawnigan Lake, BC, Canada*

selection into these orders, we can examine an animal's preference for resources based on what is available versus what is used at each scale, and whether selection at the finest scale is nested in higher-order selection (Kotliar and Wiens 1990, Edge et al. 2010). Because selection at one level is conditional upon another, the process of habitat selection is hierarchical (Johnson 1980). As the natural landscape becomes fragmented and resource distribution changes, it becomes important to study habitat selection at multiple spatial scales because strong selection at a large spatial scale may lead to no selection being detected at a smaller spatial scale (Beasley et al. 2007).

For some species, especially ectotherms, habitat selection at the microhabitat scale may be particularly important because their need to thermoregulate creates a dependence on site-specific structures and conditions (Row and Blouin-Demers 2006*a*). In this case, preferences at the home-range scale could reflect the greater presence of suitable microhabitats within one specific macrohabitat component. For example, a reptile may consistently choose to bask around decaying logs, whether the species is found in open fields or in sunny patches of mixed forest. This preference could be overlooked if habitat selection was examined at a single spatial scale. Therefore, when developing management plans for species at risk, it is valuable to document habitat use at several scales.

The eastern hog-nosed snake (*Heterodon platirhinos*; i.e., hog-nosed snake) is in the eastern half of North America, from Florida in the southern United States to Ontario in southern Canada. Several recent radio-telemetry studies (involving 6–17 individuals) have focused on habitat selection by hog-nosed snakes in the northeastern United States (NH, MA, NY). Similar to other species in northeastern North America (Blouin-Demers and Weatherhead 2001*a*, Row and Blouin-Demers 2006*a*, Halliday and Blouin-Demers 2016, Maddalena et al. 2020), common patterns of habitat selection of hog-nosed snakes include preference for edge habitats (LaGory et al. 2009, Buchanan et al. 2017, Vanek and Wasko 2017); forest with low canopy cover (Goulet et al. 2015, Akresh et al. 2017); and open, early-successional vegetation (LaGory et al. 2009, Vanek and Wasko 2017). None of these previous studies on hog-nosed snakes were conducted in Canada at the northernmost extent of the range of the species where it is listed as threatened by COSEWIC. Habitat loss, degradation, and fragmentation are identified as the leading threats to hog-nosed snakes in Canada (Seburn 2009). Therefore, our objective was to document habitat selection by hog-nosed snakes at the 3 spatial scales described above, to orient future land-management decisions and plans to mitigate habitat loss, degradation, and fragmentation. We expected that hog-nosed snakes in Ontario would prefer open areas that allow effective behavioral thermoregulation.

STUDY AREA

We conducted this study at 2 sites in the Long Point Region of southwestern Ontario (latitude: 42°42′11″N, longitude: 80°27′44″W; Fig. 1) in 2009 and 2010. The Long Point region is at the northern limit of the Carolinian deciduous forest zone and although there is a distinct winter season, the mean temperature for January remains relatively mild at −5.5°C. The mean annual rainfall for the region is 956 mm based on 24 years of data (Government of Canada 2019). Both study sites are 200 m in elevation and the region lacks significant topographical features. Land-use is predominantly agricultural with fragmented tracts of deciduous forest buffering each farm (Robson and Blouin-Demers 2013; Fig. 1). The dominant crops in our study area are soybean and corn. The trees are characteristic of Carolinian deciduous forest and include black walnut (*Juglans nigra*), butternut (*Juglans cinerea*), tulip-tree (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), various oak (*Quercus* spp.) and hickory species (*Carya* spp.), and sassafras (*Sassafras albidum*). Sympatric snake species include eastern foxsnakes (*Pantherophis vulpinus*), eastern ratsnakes (*Pantherophis alleghaniensis*), and common gartersnakes (*Thamnophis sirtalis*). American toads (*Anaxyrus americanus*) and Fowler's toads (*Anaxyrus fowleri*) are abundant prey in the study area. Potential predators include coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), and various birds of prey. The Long Point peninsula and a tract of forest known as Backus Woods are designated as a World Biosphere Reserve because of their extremely high biodiversity; our 2 study sites are in the immediate vicinity of this United Nations Educational, Scientific and Cultural Organization (UNESCO) site (Long Point Biosphere 2018). The 2 sites consisted of a patchwork of connected public and privately owned lands in the Big Creek–Walsingham corridor and were approximately 4 km × 3 km and 1 km × 3 km (Fig. 1).

METHODS

Radio-Telemetry

We located eastern hog-nosed snakes by searching habitat on foot. We captured by hand all individuals encountered ($n = 70$) and marked them by injecting a passive integrated transponder tag under the skin laterally and 75% down the body. We determined sex by probing the cloaca for the presence of hemipenes. Of the 70 captured hog-nosed snakes, we selected 25 healthy adults for transmitter implantation (17 females and 8 males). To maintain a transmitter to body mass ratio of 1:0.025 or less (Weatherhead and Blouin-Demers 2004), we used 2 sizes of transmitters for snakes in excess of 200 g and 360 g, respectively (Holohil SB-2T: 5.2 g, battery life of 12 months; Holohil SI-2T: 9 g, battery life of 18 months; Holohil Systems, Carp, Ontario). A local veterinarian inserted transmitters surgically in the body cavity following established techniques (Reinert and Cundall 1982, Weatherhead and Blouin-Demers 2004) with the addition of administration of a dose of Convenia Injectable (Zoetis, Parsippany-Troy-Hills, NJ, USA), a slow-release antibiotic, following surgery. We removed transmitters surgically from all snakes at the end of the study. We released snakes at their site of capture between

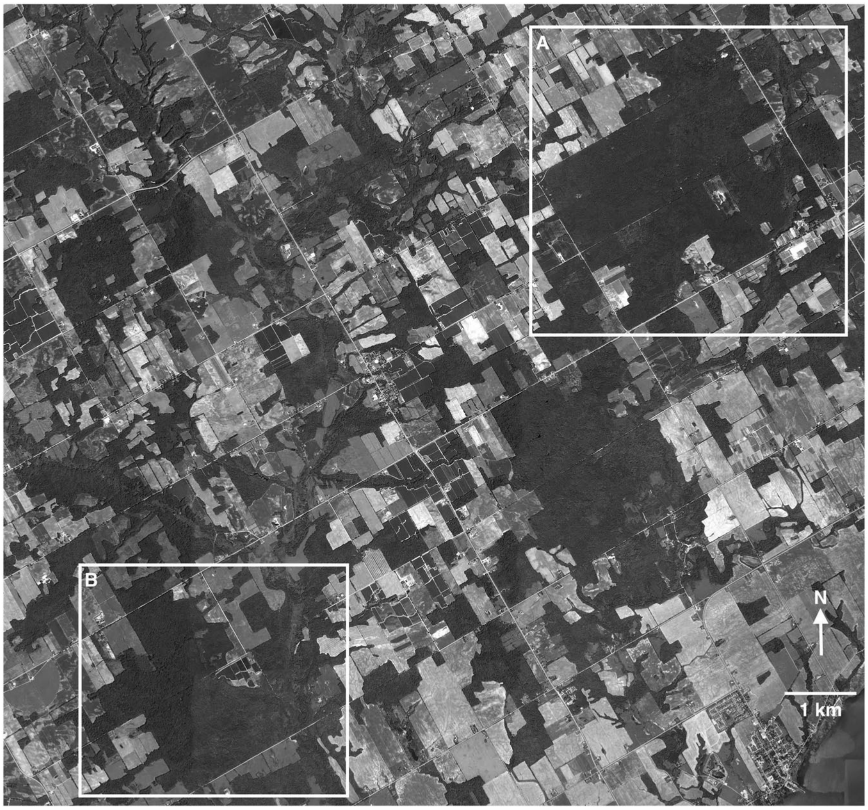

Figure 1. Study sites (A, B) for habitat selection of the eastern hog-nosed snake in the Long Point region of Ontario, Canada, 2009–2010.

24 and 48 hours following surgery. We tracked them every 5 days on average during the main activity season (1 May to 31 Aug), and then less frequently until they entered hibernacula in mid-October. At each location (the first site of contact upon relocation), we recorded the Universal Transverse Mercator coordinates using portable global positioning system units (GPSmap76Cx; Garmin International, Olathe, KS, USA) at an accuracy of <4 m. Of the 25 implanted snakes, 8 were lost to predation and thus we derived habitat selection data from 17 individuals followed over at least 1 complete active season. We cared for snakes according to the guidelines published by the Canadian Council on Animal Care (1993), with permits issued by the Ontario Ministry of Natural Resources (1058333), and under a protocol (BL-244) approved by the Animal Care Committee at the University of Ottawa.

Home Ranges

Construction of minimum convex polygons (MCPs) is the most common method to estimate home ranges (Hansteen et al. 1997, Burgman and Fox 2003, Nilsen et al. 2008) and is recommended for reptiles (Row and Blouin-Demers 2006*b*). We calculated MCPs for snakes with ≥15 telemetry locations as recommended by others (LaGory et al. 2009, Akresh et al. 2017, Buchanan et al. 2017).

One drawback of the MCP method is that it incorporates much unused area and ignores patterns of spatial and temporal selection in the home range (Burgman and Fox 2003). Kernel estimators take these patterns into account and use an algorithm that gives more weight to regions of intense use in calculating home ranges. Although MCPs are accurate estimators of home-range area for reptiles, kernel home-range estimators can be more useful in habitat selection studies. Row and Blouin-Demers (2006*b*) suggested combining the 100% MCP and kernel method to get a more accurate representation of home-range use. Thus, we adjusted the smoothing factor (h) of the kernel until the area of the 95% kernel was roughly equal to the area of the 100% MCP (±mean difference of 0.6 ha between kernel and MCP). We calculated 95% kernels and MCPs using Hawth's Tools extension (Beyer 2004) for ArcGIS version 9.2 (Esri, Redlands, CA, USA).

Landscape-Scale Habitat Selection

At the landscape scale, we characterized habitat using a land classification map created by the Ontario Ministry of Natural Resources (OMNR 2008). We collapsed the original 25 land classes into 8 habitat components: agricultural land, deciduous forest, coniferous forest, mixed forest, wetland, sand dunes, anthropogenic lands (mostly residential yards), and tree plantations. The definition of each category is provided by the OMNR (2008). For instance, our mixed forest category was a merger of mixed forest, mainly deciduous category (largely continuous forest canopy composed of coniferous and deciduous species, with deciduous species dominant; i.e., comprising >50% of the canopy) and of the mixed forest, mainly coniferous category (largely continuous forest canopy composed of coniferous and deciduous species, with coniferous species dominant; i.e., comprising >50% of the canopy), which was mostly planted pine species (*Pinus* spp.) in our study area.

To characterize the nature of habitat selected by hog-nosed snakes on the study landscape, we compared habitat components available to those occurring within the home range of every snake. This level of selection corresponds to Johnson's (1980) second order of habitat selection. We determined the habitat available to each individual by drawing a circle from the center of the MCP with a radius the length of the farthest location in the MCP from that central point (Row and Blouin-Demers 2006*a*). We then calculated the percentage of each of the 8 habitat components within the circle and within the 95% kernel home range for each individual. Because the proportions of all 8 habitat components sum to 1, the use of all habitat proportions is redundant because the value of the eighth proportion can be calculated from the values of the previous 7 proportions. To remove this linear dependency, we used a log-transformation that centers each observation on the log-transformed mean of all observations (Aebischer et al. 1993). We used the wetland habitat component as the denominator in this transformation because it was present in equal proportions in the used and available habitats of all snakes. We then performed a multivariate analysis of variance on the transformed data to test for non-random habitat selection.

We analyzed preferences for habitat components using a compositional analysis (Aebischer et al. 1993). Radio-telemetry data face the problem of non-independence because each location is related spatially to the previous location. Compositional analysis solves this issue by considering the animal as the sample unit (Aebischer et al. 1993). When habitat use was non-random, we created a matrix comparing all possible habitat-component pairs and gave ranks to each component based on preferential use using *t*-tests. Although several snakes were monitored over 2 seasons, we chose to use 1 annual home range per individual, chosen randomly, in the analysis to avoid pseudoreplication (12 females and 5 males).

Hog-nosed snakes are oviparous and females dig their nests in exposed sand dunes (Platt 1969, Cunnington and Cebek 2005, Peet-Paré and Blouin-Demers 2012). Therefore, female and male snakes may exhibit an overall difference in habitat use because females must spend approximately 2 weeks of the summer migrating towards and then nesting in open-canopy sand dunes. Because of this potential difference and its documentation in other species (Blouin-Demers and Weatherhead 2002, Hyslop et al. 2014), we always tested for the effect of sex in our analyses.

Home-Range-Scale Habitat Selection

We examined whether hog-nosed snakes selected specific land covers within their home ranges by comparing the proportion of available habitat components within the 95% kernel home range to those used for each snake. We calculated used habitat as the percentage of telemetry locations within each habitat component. This level of selection corresponds with Johnson's (1980) third-order habitat selection. The habitat components were the same as in the landscape-scale analysis. We again used a compositional analysis to examine preferences for habitat components (Aebischer et al. 1993).

Microhabitat-Scale Habitat Selection

At every second site where we located a snake, we conducted a detailed characterization of the site. We chose not to characterize habitat at sites where we found snakes traveling because these locations might not represent a true habitat choice. We waited to characterize a location until the snake had departed to avoid disturbance. We included 22 structural and vegetative components in microhabitat characterization (Table 1, detailed description for each variable is available online in Supporting Information). We then measured these same variables at paired random locations selected by walking 100 m (mean distance moved between locations by hog-nosed snakes at our study site) in a randomly determined direction (determined by blindly spinning the bearing dial on a compass) from the used sites. We characterized random locations immediately following the corresponding used location to ensure the measured variables were not affected by environmental or seasonal changes.

We used a matched-pairs logistic regression to measure microhabitat selection. Pairing the data ensured that we compared used sites to random sites that were actually available to each individual spatially and temporally (Compton et al. 2002). We interpreted the model in terms of differences in characteristics at used versus available sites (Compton et al. 2002).

An assumption of logistic regression is that each observation is independent. Using radio-telemetry locations creates the problem of pseudoreplication, where one individual's habitat choice is represented many times in the data set. It is difficult to avoid pseudoreplication when too few locations are characterized for an individual animal to be considered a unit (Aebischer et al. 1993). We collected detailed microhabitat data for 12 females and 5 males. Because no individual represented a large proportion of the total locations (median = 6%, maximum = 9%), no individual snake could have excessively biased the results.

We ran each microhabitat variable through univariate analyses, and selected those with P values < 0.25 as candidates for successive multivariate analyses (Hosmer and Lemeshow 2000). We fitted variables into test models using backward stepwise regression to select the simplest model with the highest R^2 and lowest Akaike's Information Criterion (AIC) score. Finally, we evaluated the fit of the model using the likelihood-ratio statistic (LR_2; Hosmer and Lemeshow 2000).

We conducted the compositional analyses using the computer program Resource Selection Analysis Software for Windows (version 8.1, http://www.uidaho.edu/~leban831, accessed 5 Jan 2011); we performed the matched-pairs logistic regressions in R (R version 2.12.0, www.r-project.org,

Table 1. Variables measured at used and random locations in the habitat selection analysis of 17 eastern hog-nosed snakes tracked with radio-telemetry in the Long Point Region of Ontario, Canada, 2009–2010.

Variable	Radius (m)	Description
% grass	1	Coverage (%) by live or dead grass within plot
% leaf	1	Coverage (%) by leaf litter within plot
% sand	1	Coverage (%) by sand within plot
% suspended foliage	1	Coverage (%) by living suspended foliage within plot
% woody	1	Coverage (%) by woody debris within plot
Slope angle	1	Angle of the slope (° elevation)
Slope aspect	1	Aspect of the slope (compass °)
Logs	5	Number of logs ≥7.5 cm dbh within plot
Suspended snags	5	Number of suspended snags within plot
Trees <7.5	5	Number of trees with <7.5 cm dbh in plot
Trees 7.5–15	10	Number of trees ≥7.5 and <15 cm dbh in plot
Trees 15–30	10	Number of trees ≥15 and <30 cm dbh in plot
Trees 30–45	10	Number of trees ≥30 and <45 cm dbh in plot
Trees >45	10	Number of trees ≥45 cm dbh in plot
Closest log	30	Closest distance to a log (≥7.5 cm dbh) in plot
Distance to overstory	30	Closest distance to an overstory tree (≥7.5 cm dbh) in plot
Distance to understory	30	Closest distance to an understory tree (<7.5 cm dbh) in plot
Canopy height	30	Average height of canopy (m) within plot
Distance to edge	100	Distance to edge habitat (m) from plot
Edge type	100	Type of edge transition (natural or artificial)
% closed canopy	45	Coverage (%) of arboreal canopy within a 45-degree cone

accessed 15 Mar 2011). We conducted all other statistical analyses using JMP (JMP version 5.0.1a, SAS Institute, Cary, NC, USA). We used a significance level of $\alpha = 0.05$ for all tests and we present means $\pm$ 1 standard error.

RESULTS

Based on MCPs, the mean home-range area of the 17 eastern hog-nosed snakes tracked for a whole active season was 39.4 ± 6.3 ha. Male home ranges ($n = 5$; 33.3 ± 11.9 ha, range = 9.8–59.0 ha) were slightly smaller than female home ranges ($n = 12$; 42.0 ± 7.6 ha, range = 12.3–89.8 ha).

Hog-nosed snakes used habitat nonrandomly at the landscape scale ($\chi^2_6 = 29.43$, $P \leq 0.001$). Home ranges of hog-nosed snakes incorporated sand dunes significantly more than all other habitat components with the exception of anthropogenic lands (Table 2). Home ranges encompassed agricultural land less than all other habitat components with the exception of coniferous forest (Fig. 2).

Home ranges of male and female hog-nosed snakes differed in habitat composition (Wilks' $\lambda = 0.32$, $F_{14, 50} = 2.71$, $P = 0.01$). Thus, we conducted separate compositional analyses for the 2 sexes. Selection was evident among adult females; the proportion of habitat components encompassed within home ranges was significantly different from the

Table 2. Ranking matrices comparing the composition of the home range to the habitat available in the surrounding landscape for 17 eastern hog-nosed snakes tracked with radio-telemetry in the Long Point region of Ontario, Canada, 2009–2010. Cells indicate positive or negative selection from compositional analysis log-ratios, and triple-signs represent significant selection based on pairwise t-values at $\alpha < 0.05$. Habitat components are ranked in decreasing order of selection (1 = highest; 7 = lowest).

	Habitat component							
	Sand dune	Anthropogenic land[a]	Mixed forest[b]	Tree plantation	Deciduous forest	Coniferous forest	Agricultural land	Rank
All snakes ($n = 17$)								
Sand dune	0	+	+++	+++	+++	+++	+++	1
Anthropogenic land	−	0	+	+	+	+++	+++	2
Mixed forest	− − −	−	0	+	+	+	+++	3
Tree plantation	− − −	−	−	0	+	+	+++	4
Deciduous forest	− − −	−	−	−	0	+	+++	5
Coniferous forest	− − −	− − −	−	−	−	0	+	6
Agricultural land	− − −	− − −	− − −	− − −	− − −	−	0	7
Females only ($n = 12$)								
Sand dune	0	+++	+++	+	+++	+++	+++	1
Anthropogenic land	− − −	0	+	−	+	+	+++	3
Mixed forest	− − −	−	0	−	+	+	+++	4
Tree plantation	−	+	+	0	+	+	+++	2
Deciduous forest	− − −	−	−	−	0	+	+++	5
Coniferous forest	− − −	−	−	−	−	0	+	6
Agricultural land	− − −	− − −	− − −	− − −	− − −	−	0	7

[a] Anthropogenic land including residential sites.
[b] Mixed deciduous and coniferous forest.

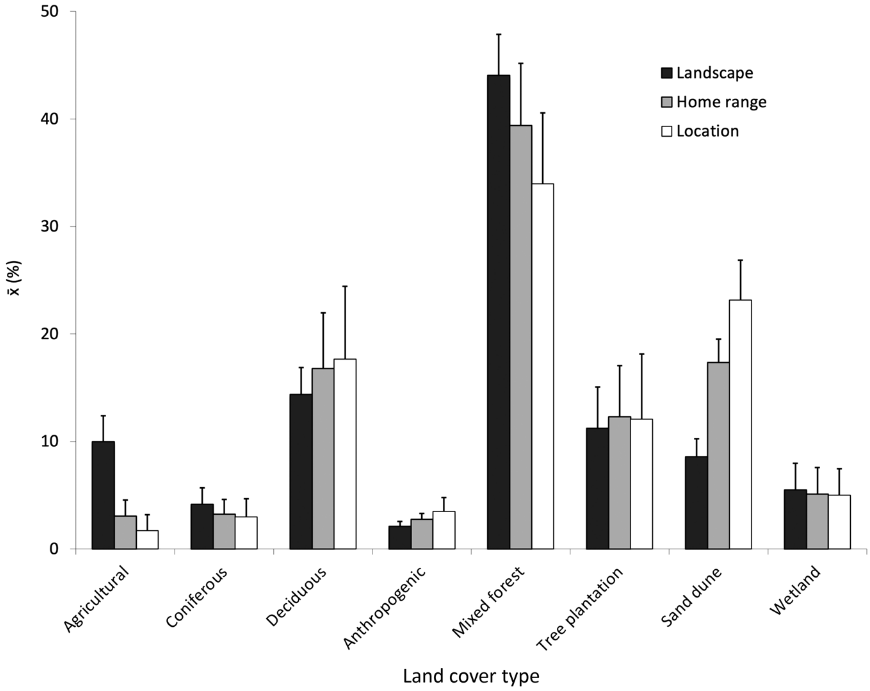

Figure 2. Percent ($\bar{x} \pm$ SE) of the 8 habitat components within the landscapes surrounding the 95% kernel home ranges, within the 95% kernel home ranges, and at the locations used by 17 adult eastern hog-nosed snakes tracked in the Long Point region of Ontario, Canada, 2009–2010.

proportion of those habitat components available in the adjacent landscape ($\chi^2_6 = 27.85$, $P \leq 0.001$). Female snakes incorporated sand dune habitat in their home ranges significantly more than all other habitat components except tree plantation, which was included less but not significantly so (Table 2), whereas agricultural land was included in home ranges significantly less than other habitat components with the exception of coniferous forest (Table 2). We had too few male snakes to conduct a compositional analysis because the number of individuals must equal or exceed the number of habitat components (Aebischer et al. 1993).

To allow comparison between patterns at the landscape and home-range scales, we used data from each individual snake at both scales. At the home-range scale, we found no significant difference in the way male and female snakes selected habitat components within their home ranges ($\lambda = 0.47$, $F_{14} = 1.63$, $P = 0.10$). Hog-nosed snakes preferred certain habitat components within their home ranges ($\chi^2_6 = 17.13$, $P = 0.005$). Snakes were located on anthropogenic land at a higher frequency than these habitat components were available within their home ranges (Fig. 2; Table 3).

We characterized microhabitat at 106 locations used by snakes (78 by females, 28 by males) and 106 paired random locations. Six variables contributed to the model with the lowest AIC value (Table S1, available online in Supporting Information). Snakes preferred microhabitats with more woody debris, with more suspended foliage, closer to the nearest understory tree, with more logs, and with fewer trees 30–45 cm in diameter and >45 cm in diameter (AIC = 92.2, $LR_2 = 66.8$, $P \leq 0.001$; Table 4). The best model for females included 4 variables. Females preferred microhabitats with

Table 3. Ranking matrix comparing used locations to the composition of the home ranges for 17 eastern hog-nosed snake tracked with radio-telemetry in the Long Point region of Ontario, Canada, 2009–2010. Cells indicate positive or negative selection from compositional analysis log-ratios, and triple-signs represent significant selection based on pairwise t-values at $\alpha < 0.05$. Habitat components are ranked in decreasing order of selection (1 = highest; 7 = lowest).

	Habitat component							
	Sand dune	Anthropogenic land[a]	Mixed forest[b]	Tree plantation	Deciduous forest	Coniferous forest	Agricultural land	Rank
All snakes ($n = 17$)								
Sand dune	0	−	+	−	+	−	−	5
Anthropogenic land	+	0	+++	−	+	+	+	2
Mixed forest	−	− − −	0	−	−	− − −	−	7
Tree plantation	+	+	+	0	+	+	+	1
Deciduous forest	−	−	+	−	0	−	−	6
Coniferous forest	+	−	+++	−	+	0	+	3
Agricultural land	+	−	+	−	+	−	0	4

[a] Anthropogenic altered land including residential sites.
[b] Mixed deciduous and coniferous forest.

Table 4. Coefficients (±SE) and odds ratios for a matched-pairs logistic regression model explaining microhabitat use by 17 eastern hog-nosed snakes tracked with radio-telemetry in the Long Point Region of Ontario, Canada, 2009–2010.

Variable	Coefficient	SE	Increase	Odds ratio	Odds ratio 95% CI
% woody debris	0.0426	0.022	1%	1.0435	(0.999, 1.09)
% suspended foliage	0.0466	0.013	1%	1.0477	(1.02, 1.07)
Trees 30–45 cm dbh	−0.3837	0.104	1 tree	0.6813	(0.56, 0.84)
Tree >45 cm dbh	−0.7749	0.238	1 tree	0.4608	(0.29, 0.74)
Distance to understory	−0.0008	0.001	0.01 cm	0.9992	(0.998, 1.00)
Number of logs	0.1222	0.789	1 log	1.1299	(0.97, 1.32)

more woody debris, more suspended foliage, more trees 30–45 cm in diameter, and more canopy closure (AIC = 68.6, $LR_2 = 47.53$, $P \leq 0.001$). Males differed slightly from females with the distance to an overstory tree (preferring to be farther) replacing canopy closure in the model (AIC = 27.5, $LR_2 = 19.3$, $P < 0.007$).

DISCUSSION

The mean MCP home-range area we calculated for eastern hog-nosed snakes in Ontario (39 ha, $n = 17$ snakes) is comparable to most previously reported values for populations in the northeastern United States: 52 ha (LaGory et al. 2009), 35 ha (Buchanan et al. 2017), 25 ha (Vanek and Wasko 2017), and 19 ha (Akresh et al. 2017). Goulet et al. (2015) reported larger home ranges, averaging 73 ha, in New Hampshire. Goulet et al. (2015) is also the only study where hog-nosed snakes used closed-canopy forest extensively. It is possible that closed-canopy forest is a poor-quality habitat for hog-nosed snakes, potentially because of the scarcity of basking sites. Thus, larger home ranges may be required to access required resources in closed-canopy forest.

It is evident that hog-nosed snakes in our study area used the environment non-randomly at all 3 spatial scales examined. Home ranges of hog-nosed snakes included open-canopy environments like sand dunes, plantations of young trees, and anthropogenic lands more frequently than denser, closed-canopy land cover types like deciduous and coniferous forest. These results are consistent with the habitat selection patterns documented in most recent studies on the species in the northeastern United States (LaGory et al. 2009, Akresh et al. 2017, Buchanan et al. 2017, Vanek and Wasko 2017). Sand dunes are exceptionally important for female hog-nosed snakes because the snakes rely on areas with sandy soils and abundant solar radiation to incubate their eggs throughout the summer months (Peet-Paré and Blouin-Demers 2012). Preference by hog-nosed snakes for tree nurseries, plantations, and anthropogenic lands may reflect opportunities for basking within edge habitats that allow light penetration but also provide structures for concealment.

Within their home ranges, hog-nosed snakes used slightly different habitat components than at the larger, landscape scale. Tree plantations ranked ahead of human-altered habitats, like roads and residential areas. Coniferous forest ranked third followed by agricultural land in the order of preference owing to the use of edge habitat along crop fields rather than use of the fields themselves. In fact, a *post hoc* analysis revealed that hog-nosed snakes were never located in fields farther than 5 m from their edges, and only 8 of 326 locations were in fields. Sand dunes were used by female hog-nosed snakes only during the short nesting period in June; thus, it is logical that they ranked lower in preference at the scale of the home range. Snakes appeared to use anthropogenic lands within their home ranges as basking areas in addition to natural open sites like sand dunes and forest breaks. It is possible that fire suppression over the last several decades has allowed succession to occur in our study area and has led to a reduction of the proportion of open areas owing to forest encroachment. Coniferous forest was also used more frequently within home ranges. At our study site, eastern white (*Pinus strobus*) and red pine (*P. resinosa*) were planted in the 1930s in uniform stands (Draper et al. 2002), which, for the most part, remain intact presently. When a mature tree falls from wind or disease in this type of even-aged stand, a large gap results in the canopy, whereas in an uneven-aged forest with canopy trees of varying heights, the effect of 1 fallen tree on conditions on the forest floor may be less pronounced. On our study sites, snakes used locations within their home ranges where downed pines created openings in the plantation canopy.

Microhabitat selection by hog-nosed snakes was also clear with a model for all snakes combined showing preferences for locations characterized by woody debris, understory vegetation like saplings, raspberries (*Rubus* sp.), ferns, and graminoids, and farther from mature trees. Female snakes chose locations with more woody debris and foliage, more mature trees, and greater canopy cover than randomly sampled sites. Selection for microhabitats with high structure may be a response to high risk of predation given that many snakes were eaten by predators. Nesting sites were not included in this microhabitat analysis. Therefore, after oviposition, thermoregulation through basking may become less important for females. Blouin-Demers and Weatherhead (2001*b*) reported that female grey rat snakes (*Pantherophis spiloides*) maintained body temperatures higher by approximately 2°C prior to oviposition than after. Another explanation may be that following the nesting season, the ambient daytime temperature remains consistently high (>25°C) in this region of Ontario, so females may not need to bask in direct sun to maintain optimal body temperatures.

Thermoregulation dictates the activity patterns and behavior of many ectotherms (Mullin and Seigel 2009, Halliday and Blouin-Demers 2016). Hog-nosed snakes are oviparous and mature females can develop up to 42 eggs (Peet-Paré and Blouin-Demers 2012). Vitellogenesis takes several weeks during which time the female's metabolic rate must be elevated (Birchard et al. 1984, Ladyman et al. 2003); choosing locations, typically open ones, that allow effective thermoregulation is likely more important for females than for males during this time of year.

Gravid hog-nosed snakes use sand barrens for about 2 weeks, but eggs remain buried in dunes for approximately 6 weeks (Peet-Paré and Blouin-Demers 2012) where they are vulnerable to human activity, as are emerging neonates. The use of all-terrain-vehicles was prevalent throughout the summer in the open dunes where nesting took place. Reproductive individuals are key for population viability (Shine and Bonnet 2000) and during the nesting season female snakes make long distance movements to arrive at the nesting sites, which puts them at greater risk of predation and road mortality (Robson and Blouin-Demers 2013). Incompatible land use, especially in sensitive areas, does not bode well for adult survival, nest-site viability, or juvenile recruitment of this threatened species.

MANAGEMENT IMPLICATIONS

Warm open areas, especially sites with sandy soils, are key to the life history of hog-nosed snakes, but succession converts such open areas into closed forest. Therefore, active management, such as prescribed burns or cutting vegetation, may be required to maintain them. Appropriate conservation measures should also be put in place on public lands to ensure recreational activities, such as use of all-terrain-vehicles, do not damage required habitat components, injure snakes, or destroy eggs. Hog-nosed snakes often associate with land cover types created and regularly used by humans, which puts them at risk of being killed incidentally and directly by people. Therefore, citizen awareness and education represent other important conservation tools.

ACKNOWLEDGMENTS

We thank C. A. Peet-Paré for her invaluable help with fieldwork. M. E. Gartshore, P. J. Carson, and S. D. Gillingwater provided much information that helped us locate snakes initially. We are grateful to the late C. E. Crombie and to all the support staff from Windrush Veterinary Services in Brantford, Ontario for performing the surgeries. We are indebted to C. A. Paszkowski for her extremely detailed and thoughtful reviews of our manuscript. Funding for this study was provided by the University of Ottawa, Parks Canada, the Species at Risk Fund of Ontario, and the Natural Sciences and Engineering Research Council of Canada.

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Associate Editor: Cynthia Paszkowski.

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