The spatial ecology of Eastern Hognose Snakes (*Heterodon platirhinos*): habitat selection, home range size, and the effect of roads on movement patterns

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ABSTRACT

Habitat loss is the greatest contributor to the decline of species globally and thus understanding habitat use and the consequences fragmentation has on biodiversity is a fundamental step towards management and recovery. I conducted a radio-telemetry study to examine the spatial ecology and the effects of roads on Eastern Hognose Snakes (*Heterodon platirhinos*), a species at risk, in the Long Point Region of Ontario, Canada. I tested habitat selection at multiple spatial scales and I found that within the home range, snakes avoided agricultural land and selected open sand barrens, particularly for nesting. At the local scale, snakes avoided mature overstory trees and used younger patches of forest. Used locations had more woody debris, logs and low-vegetative coverage than locations selected at random. Eastern Hognose Snakes also showed avoidance of paved road crossings in their seasonal movements, but readily crossed unpaved roads. Management efforts for this species at risk should be placed on the conservation of sand barrens and on the construction of road underpasses to prevent genetic isolation of populations.

RÉSUMÉ

Globalement, la perte d'habitat est le plus grand facteur contribuant à la baisse de la biodiversité. Comprendre l'utilisation des habitats et les effets de la fragmentation de ceuxci sur la biodiversité est donc une étape fondamentale dans la gestion et le rétablissement des espèces. J'ai réalisé une étude de radiotélémetrie concernant l'écologie spatiale et l'effet des routes sur la couleuvre à nez plat (Heterodon platirhinos), une espèce en péril, dans la région de Long Point en Ontario, Canada. J'ai étudié la sélection d'habitat à plusieurs échelles spatiales et j'ai trouvé qu'à l'échelle du domaine vital, les couleuvres ont évité les terres agricoles, mais sélectionné les dunes de sable sans couvert, en particulier pour la nidification. Au niveau du microhabitat, les couleuvres ont évité les forêts matures d'arbres dominants et utilisé des parcelles de forêt jeune. Les emplacements utilisés avaient plus de débris ligneux, de bûches et un couvert végétal bas comparativement aux emplacements choisis au hasard. Les couleuvres à nez plat ont aussi évité la traversée de routes pavées dans leurs déplacements saisonniers, mais ont fréquemment traversé des routes non pavées. Pour protéger cette espèce en péril dans le futur, les efforts de gestion devraient être mis sur la conservation des habitats sablonneux et sur la construction de passages souterrains sous les routes pour éviter l'isolement génétique des populations.

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GENERAL INTRODUCTION

Loss of Biodiversity and Conservation Law

Biodiversity is being lost worldwide and while species extinctions are natural phenomena, the current rate of extinction is exceptionally higher than any other period in history (Raup & Sepkoski 1984). It has become apparent that this global loss of biodiversity is the consequence of anthropogenic pressure on the environment (Gibbons *et al.* 2000, Aitken 1998). Ecologists agree that the single greatest threat to terrestrial wildlife is habitat destruction and degradation (Soule 1991, Wilcove *et al.* 1998, Hanski 2005). The degradation of suitable habitat can directly result in the extirpation of local populations from an area but, more commonly, fragmented landscapes leave insufficient space and resources for populations to exist (Hanski 2005, Fahrig 2003). Road construction contributes to habitat fragmentation and places additional pressure on animals that migrate to access resources, mates, and breeding grounds. When roads bisect suitable habitat, animals are either faced with a greater risk of road mortality by crossing or genetic isolation if they choose to avoid them.

Legislation has been enacted in many countries, territories, states, and provinces that protect species at risk in an effort to slow the global decline of biodiversity. In Canada, the Species at Risk Act (SARA 2003) protects listed species at risk on federal land. In the province of Ontario, further protection is given to species at risk on provincial land under the Ontario Endangered Species Act (OESA 1971, 2007). While these acts offer direct protection to species, they offer no

protection to the habitat they occupy until an official definition of 'critical habitat' exists. For any species listed under SARA or the OESA, a recovery strategy must be created (SARA 2003, OESA 1971, 2007) to identify threats facing a species or population and to define the habitat critical to its survival. Once critical habitat is defined for a species, it too is given federal and in the case of Ontario, provincial protection. Thus, recovery strategies play a key role in the ground-level management decisions made to protect and aid in the recovery of species at risk (Boersma *et al.* 2001).

Reptile Populations in Decline

Reptiles face unique conservation challenges because they are not highly mobile compared to mammals and birds. In Canada, reptiles are proportionally the most at-risk group of animals (SARA 2011). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) lists 17 of 25 (68%) resident snakes as species-at-risk. The protection of these species-at-risk in Canada largely depends on reliable scientific information so that appropriate recovery and conservation plans may be developed, but in the case of reptiles basic life-history information is often lacking because they lead cryptic lives and are difficult to study (Lagory *et al.* 2009, Mullin & Seigel 2009).

In 2001, the Eastern Hognose Snake (*Heterodon platirhinos*) was listed as *Threatened* in Canada by COSEWIC. A recovery strategy for *H. platirhinos* was finalized in March 2009 outlining the necessary actions to secure this species' long-term persistence in the wild; however, critical habitat has yet to be defined for this

species. Habitat loss, degradation, and fragmentation are believed to be the leading threats for populations of *H. platirhinos* (Seburn 2009). Eastern Hognose Snakes belong to the genus *Heterodon* that occur solely in North America (Conant & Collins 1998). They are large-bodied and females produce up to 43 eggs (Peet-Paré 2010). In Ontario, two distinct populations exist: in the Georgian Bay to Peterborough corridor and in southwestern Ontario, but it is unknown whether these populations are genetically isolated. Previous studies have found selection towards sand barren habitat likely because females require sand to dig and lay their eggs (Michener & Lazell 1989).

Objectives

The aim of my thesis is to study the effects of anthropogenic change on the spatial ecology of a population of Eastern Hognose Snakes (*H. platirhinos*), a species at risk in Canada, and to contribute meaningful information toward future management of habitat for this species. In Chapter 1, I examined habitat use at multiple spatial scales to determine what habitat types Eastern Hognose Snakes select, if any habitat type is avoided, and at what scale do they select these features. I discuss anthropogenic pressures on Eastern Hognose Snakes and the effects road networks have on snake movements in Chapter 2. It is my hope that by identifying important habitat characteristics at both the macrohabitat and microhabitat scales, as well as sources of genetic isolation; future development and management plans may mitigate threats to Eastern Hognose Snake habitat better.

CHAPTER I

Habitat selection of the Eastern Hognose Snake (*Heterodon platirhinos*) at multiple spatial scales in the Long Point Region of Ontario, Canada.

Abstract

Habitat loss is the greatest contributor to the decline of species globally and thus documenting habitat use is a fundamental step towards management and recovery. All animals have a choice as to the type of habitat they use for conducting their central activities. Because the availability of different resources and habitat types within a landscape is scale dependent, their use should be examined at multiple spatial scales. I conducted a radio-telemetry study to examine habitat selection at multiple spatial scales by Eastern Hognose Snakes (Heterodon platirhinos), a species at risk, in the Long Point Region of Ontario, Canada. At the home range scale, Hognose Snakes avoided agricultural land and selected open sand barrens, particularly for nesting. At the scale of the location, snakes avoided mature overstory trees and used younger patches of forest. Used locations had more woody debris, logs and low-vegetative coverage from raspberries, ferns and graminoids than locations selected at random. Since Eastern Hognose Snakes rely on open sandy habitat for nesting, management efforts should be placed on the conservation of inland sand barrens and shoreline sand dunes.

Introduction

At the global scale, habitat destruction is the leading cause of species decline and extinction (Taylor *et al.* 2011). Different animals have different habitat needs; however what is common between all species is that when resources are reduced or

the condition of habitat degrades, viable populations cannot be sustained (Hanski 2005). In a changing environment where land is being converted for agricultural use or urban development, it becomes increasingly important to save wild spaces for wildlife. Forest fragments, left over after development, may leave insufficient space and resources for a population or even one territorial animal to persist (Hanski 2005, Fahrig 2003).

Status of reptile populations

Reptiles face unique conservation challenges because they are not highly mobile compared to mammals and birds. Thus, industrial and urban developments that fragment the landscape into isolated patches can be particularly detrimental to reptile populations (Fahrig 2003). This is especially true in Canada where the ranges of many reptiles overlap the most densely populated and urbanized regions (Mullin & Seigel 2009). In these areas, not only is forest habitat fragmented, but snakes also face the additional pressures of human development like road mortality and persecution (Seburn 2009). It is not surprising, then, that reptiles are proportionally the most at-risk group of animals in Canada (SARA 2011). In fact, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) lists 17 of 25 (68%) resident snakes as species-at-risk. The protection of these species-at-risk in Canada largely depends on reliable scientific information so that appropriate recovery and conservation plans may be developed, but in the case of reptiles basic life-history information is often lacking because they lead cryptic lives and are difficult to study (Lagory et al. 2009, Mullin & Seigel 2009).

Orders of habitat selection

All animals have a choice in selecting the habitat in which they live. Habitat selection can span multiple spatial scales (Owen 1972) and thus studies aiming to delineate habitat use should encompass as many levels as possible. First-order selection defines the geographic range of the species, second-order selection distinguishes the home range within that landscape and third-order selection establishes which specific habitat components the species uses within the home range (Johnson 1980). By dividing habitat selection into these orders we can examine an animals' preference for resources based on what is available versus what they use at each scale and whether selection at the finest scale is nested in higher-order selection (Kotliar & Wiens 1990). Since 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 more important to determine whether a species selects habitat by a hierarchical process (Beasley *et al.* 2007). Some species, especially ectotherms, may only select habitat at the micro scale because their need to thermoregulate creates a dependence on site-specific structures and conditions (Row & Blouin-Demers 2006b). In this case, preferences found at the home range scale could be a result of a greater presence of suitable microhabitat within one specific macrohabitat type. For example, a reptile may consistently choose to bask around decaying logs, whether they are found in open fields or in sunny patches of mixed

forest. This preference could not be observed if only a single scale was measured. Therefore, when developing management plans for species-at-risk it is imperative to document the habitat needs of these animals at the landscape, macro- and microspatial scales. Several recent studies have focused on reptile habitat selection at multiple spatial scales (Row & Blouin-Demers 2006b, Harvey & Weatherhead 2006 and Carrière & Blouin-Demers 2010); however none have focused on the Eastern Hognose Snake (*Heterodon platirhinos*), a species listed as *Threatened* by COSEWIC, within its Canadian range. Habitat loss, degradation, and fragmentation are the leading threats for *H. platirhinos* in Canada (Seburn 2009). Thus, the focus of this paper is to study habitat selection at three spatial scales for *H. platirhinos* in the Long Point region of Ontario, Canada so that appropriate land management decisions may be made in the future to mitigate these threats.

Habitat selection by Eastern Hognose Snakes

Previous studies of *H. platirhinos* in New York and New Hampshire found that Eastern Hognose Snakes prefer upland sandy pine forests, old-fields and forest edge habitat at the home range scale (Michener & Lazell 1989, Lagory *et al.* 2009). These studies did not detect selection at the microhabitat scale, however, probably because few site-specific variables and no structural characteristics were measured. I expected Eastern Hognose Snakes to use their habitat nonrandomly at both the microhabitat and macrohabitat scales. Snakes are ectothermic and thus need to balance thermoregulation with foraging and predator avoidance so I expected that *H. platirhinos* would choose sites with lower canopy cover and structures like logs

and snag to balance basking and retreat opportunities. Females are oviparous (Platt 1969) and therefore have a greater need to bask early in the active season while their eggs develop, so at the macrohabitat scale I expected that females would use edge habitat more than males.

Methods

Study site

I conducted this study at two sites in the Long Point Region of southwestern Ontario, Canada (Latitude: 42° 42' 11" N Longitude: 80° 27' 44" W). Field research took place from May to October in 2009 and in 2010. The St. Williams Conservation Reserve, approximately 4 km x 3 km, was used as one site and the other 1 km x 3 km area was a patchwork of connected public and privately owned lands in the Big Creek –Walsingham corridor (Fig. 1-1). Animals were cared for according to the guidelines in the *Guide to the Care and Use of Experimental Animals* published by the Canadian Council on Animal Care, 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.

Radio-telemetry

I located Eastern Hognose Snakes by searching appropriate habitat. All snakes encountered (n = 70) were captured by hand and were marked by injecting a sub-dermal Passive Integrated Transmitter (PIT) in their hindquarter. Sex was

distinguished by probing the cloaca for presence of hemipenes.

Of the captured snakes, I selected 25 healthy adults for transmitter implantation (17 females and 8 males). To maintain a transmitter to body weight ratio of 1:0.025 or less, two sizes of transmitters were used for snakes in excess of 200 g and 360 g, respectively (Holohil SB-2T: 5.2g, battery life: 12 months; Holohil SI-2T: 9 g, battery life of 18 months; Holohil Systems Ltd., Carp, Ontario, Canada). Transmitters were inserted surgically by a local veterinarian following the Reinert technique (Reinert & Cundall 1982) with one amendment: administration of a Convenia Injectable (Pfizer Animal Health) slow-release antibiotic post-surgery. Transmitters were removed from all snakes at the end of the study. Snakes were released at their site of capture between 24 – 48 hr following surgery and were tracked every 5.3 days on average during peak activity season (1 May to 31 August). At each location, the Universal Transverse Mercator (UTM) coordinates were recorded using GPSmap76Cx portable GPS units (Garmin International Inc., Olathe, KS) at an accuracy of <4 m. Snakes were tracked from their implantation until they entered hibernacula in mid-October. Of the 25 implanted snakes, some were lost to predation thus habitat selection data was derived from 17 individuals for which movement was recorded over one complete active season. The majority of transmitter snakes were located on the St. Williams Conservation Reserve despite equal search effort on both properties thus comparisons of habitat selection and landscape composition between the two locations are not warranted.

Home ranges

Minimum convex polygons (MCPs) are the most common method to estimate home ranges (Nilsen et al. 2008, Burgman & Fox 2003, Hansteen et al. 1997). An MCP is calculated by drawing the smallest possible convex polygon from all known locations recorded for an animal. I calculated MCPs for snakes with a minimum of fifteen telemetry locations. No standard rule has been set for the minimum number of repetitions needed to accurately calculate home range using MCPs and a wide range exists in the literature. However Galbraith et al. (1987) used as few as 16 repetitions in a study of male Snapping Turtle (Chelydra serpentina) home range. I chose fifteen to balance the trade-offs between number of individuals tracked and number of observations per individual. One downfall of the MCP method is that it incorporates much unused area and ignores patterns of spatial and temporal selection in the home range (Burgman & 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. While MCPs have been shown to be accurate estimators of home range size for reptiles, kernel home-range estimators can be more useful in habitat selection studies. Row and Blouin-Demers (2006a) suggested combining the 100% MCP and kernel method to get a more accurate representation of home range. I followed this method and 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 (Kernel-MCP ± mean difference of 0.6 ha). Kernels and MCPs were calculated using Hawth's Tools extension (Beyer 2004) for ArcGIS version 9.2 (Environmental Systems Research Institute, Redlands, CA, 2006).

Macrohabitat selection

Macrohabitat was characterized using a land classification map created by the Ontario Ministry of Natural Resources (SOLRIS 2008). The original 25 land classes were generalized and collapsed into 8 habitat types: agricultural land (CROP), deciduous forest (DECID), coniferous forest (CONIF), mixed forest (MIXED), wetland (WETLD), sand dunes (SAND), human altered landscape (ALTER) and tree plantations (PLANTA).

To assess habitat selection at the macrohabitat scale, I compared the available habitat types to those within the home range of every snake. The habitat available to each individual was determined by drawing a circle from the centre of the MCP with a radius the length of the farthest location in the MCP from that point. I then calculated the percentage of CROP, DECID, CONIF, MIXED, WETLD, SAND, ALTER and PLANTA within the circle of available habitat and the 95% kernel for each individual. Since the proportions of all eight habitat types sum to one, the use of all habitat proportions is redundant. To remove this linear dependency a logtransformation was used. Aebischer *et al.* (1993) found that for any component x_i of habitat within a composition, the log-ratio transformation $y_i = \ln(x_i / x_i)$ (where x_i is another proportion of habitat within the composition) renders the y_i linearly independent. This transformation is equivalent to centering each observation on the log-transformed mean and so the result is independent of the chosen denominator x_i (Aebischer et al. 1993). In this case, I chose the habitat type WETLD as the denominator as it was consistently available to all snakes in both the used and available habitat. I then performed a MANOVA on the transformed data to test for

non-random habitat selection between the sexes. Wilks' λ was used as the test statistic for the effects of sex and habitat type.

Preferences for habitat types were analyzed using a compositional analysis (Aebischer *et al.* 1993). Radio-telemetry data also face the problem of non-independence as each location is spatially related to the previous. Compositional analysis solves this issue by considering the animal as the sample unit over the telemetry locations (Aebischer *et al.* 1993). A compositional analysis tests for the difference between all pairs (d = yU - yA) of log-transformed used (U) and available (A) habitat proportions (y) for each animal. This analysis tests the null hypothesis that snakes use certain habitat types in proportion to their availability in the landscape (yU = yA). I created a matrix comparing all possible habitat-type pairs to give ranks to each type based on preferential use. Although several snakes were monitored over two seasons, I chose to use one single annual home range per individual in the analysis to avoid pseudoreplication (12 females and 5 males).

Microhabitat selection based on land cover

I examined whether Eastern Hognose Snakes selected locations within their home range randomly by comparing the proportion of available habitat types to those used within the 95% kernel. The percentage of area occupied by habitat types in the 95% kernel represented available habitat. Used habitat was the percentage of telemetry locations within each habitat type in the home range. I calculated the percentage of cropland (CROP), deciduous forest (DECID), coniferous forest (CONIF), mixed forest (MIXED), wetland (WETLD), sand dune (SAND) and human

altered land (ALTER) within the home range using the SOLRIS land classification map in ArcGIS 9.3 (2008). As with the macro-scale selection, I again used a compositional analysis to examine preferences for habitat types (Aebischer *et al.* 1993).

Microhabitat selection based on detailed habitat characterization

In every second site where a snake was located, I recorded the general habitat type (FOREST, FIELD, EDGE, SANDDUNE, WETLAND) and conducted a more detailed habitat characterization. General habitat type at this scale was analyzed using a \mathbf{x}^2 test. I chose not to characterize habitat at sites where snakes were found travelling as habitat used at these exact locations might not represent true choice. I waited to conduct the characterizations until the snake had departed the location so as to not cause disturbance. I included 22 structural and vegetative components in the microhabitat characterization (Table 1-1). I measured these same variables at paired random locations. I selected random locations by walking 100 m (mean distance moved between locations, Cunnington 2009 pers. com.) in a randomly determined direction (by blindly spinning the bearing disc on a compass) from the centre of a used site. Random locations were characterized immediately following the paired-used location to ensure the measured variables were not affected by environmental or seasonal changes.

I used a matched-pairs logistic regression to measure microhabitat selection within the snakes' home ranges. In this instance, a paired design is warranted

because I want to evaluate the relationship between use and availability. Pairing the data also ensures that the used site is being compared to a random site that was actually available to each individual both spatially and temporally (Compton *et al.* 2002). A standard logistic regression, with the constant term removed, is used to fit a response between presence and absence to the differences in habitat values between used and random locations. So in this case the values for each random point are subtracted from the values of each paired snake location. Therefore the estimated coefficients, β_{ij} , in a paired logistic regression are the differences between paired versus control observations. As with a standard logistic regression, an *n*-unit increase in the habitat variable results in an $e^{n\beta_i}$ increase in the odds ratio. So the model is interpreted in terms of differences in characteristics at used versus available sites use rather than absolute measured values (Compton et al. 2002).

As with the compositional analysis, another assumption of the 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. However, it is difficult to avoid pseudoreplication when too few locations are characterized for each animal to be considered a unit of its own (Aebischer *et al.* 1993). I collected detailed microhabitat-use data for 12 female and 5 male snakes. Since no individual represented a large proportion of the total locations (median = 5.88%, maximum = 9.43%), no individual snake excessively biased the group means.

Eastern Hognose Snakes are oviparous and females tend to dig their nests in open sand dune habitat (Cunnington & Cebek 2005, Platt 1969). Therefore female

and male snakes may exhibit an overall difference in microhabitat use, as females must spend several weeks of the summer migrating towards and then nesting in open-canopy sand dunes. Due to this difference I constructed separate microhabitat models for each sex. Each variable was run through univariate analyses and those with p values <0.25 were selected as candidates for successive multivariate analyses (Hosmer & Lemeshow 2000). Variables were fitted 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, the fit of the model was evaluated using the likelihood-ratio statistic (Hosmer and Lemeshow 2000).

Statistical analyses

I used the computer program Resource Selection for Windows (Leban 1999) to conduct the compositional analyses while the matched-pairs logistic regressions were performed in R version 2.12.0 (R Foundation for Statistical Computing 2010). All other statistical analyses were done using JMP version 5.0.1a (SAS Institute Inc. 2002). A significance level of $\alpha = 0.05$ was accepted for all tests.

Results

Macrohabitat selection

Eastern Hognose Snakes showed nonrandom habitat-use at the home-range scale ($\chi^2_{[6]}$ = 29.43, p < 0.0001). The compositional analysis ranked the habitat types as SAND > ALTER > MIXED > PLANTA > DECID > CONIF > CROP (Table 1-2). Sand dunes were used significantly more than all other habitat types with the exception

of altered habitat. Cropland was used significantly less than all habitat types except coniferous forest. Altered habitat was used significantly more than coniferous forest (Figure 1-2).

The MANOVA testing if male and female snakes use their habitat differently was significant (λ = 0.32, $F_{[14,50]}$ = 2.71, p = 0.01). Therefore I proceeded to conduct separate compositional analyses for the two sexes. Selection was evident amongst adult female snakes in that the proportion of used habitat types was significantly different from the proportion of those habitat types available within the home range ($\chi^2_{[6]}$ = 27.85, p <0.001). Male snakes, however, had too small a sample size to conduct a compositional analysis, as the number of individual has to at least match the number of habitat types. The ranking for habitat types in order of preference for females was: SAND > ALTER > PLANTA > MIXED > DECID > CONIF > CROP. Sand dunes were used significantly more than all other habitat types while cropland was used significantly less than all types with the exception of coniferous forest. Also, both altered habitat and tree plantations were used significantly more than coniferous forest.

Microhabitat selection based on land cover

To allow comparison between macro- and microhabitat scale analyses, I used the same individual snakes and seasonal data. According to MANOVA, male and female snakes did not select general habitat type within their home ranges differently (λ = 0.47, $F_{[14]}$ = 1.63, p = 0.10). The compositional analysis, however, showed that hognose snakes select certain habitat types preferentially from what is

available within their home range ($\chi^2_{[6]}$ = 17.13, p < 0.05). Ranked in order of preference, the habitat types snakes selected for were PLANTA > ALTER > CONIF > CROP > SAND > DECID > MIXED. Mixed forest was used significantly less than coniferous forest, sand dunes and human-altered habitat while altered habitat was used significantly more than sand dunes. When examined independently female snakes did not show significant selection within the home range ($\chi^2_{[6]}$ = 12.58 p = 0.05). Again, male snakes had too small a sample size to conduct a compositional analysis at this scale.

Microhabitat selection based on detailed habitat characterization

I characterized habitat at 106 snake sites (78 adult females, 28 adult males) and their paired 106 random sites. The model with the lowest AIC value for all snakes included 6 variables; %W00DY, %SUSFOLI, 40-45, >45, DUNDER AND #LOGS (AIC = 92.2 LR₂ = 66.8 p < 0.0001). AIC scores and weights for other tested models can are found in Table 1-3. When considered alone, the best model for adult females included %W00DY + %SUSFOLI, + 30-45 + CANCLOS (AIC = 68.6 LR₂ = 47.53 p < 0.0001). Adult males differed slightly from females with the distance to an overstory tree replacing canopy closure (%W00DY + %SUSFOLI + 30-45 + D0VER) (AIC = 27.5 LR₂ = 19.3 p < 0.007). Overstory trees from 30-45 cm dbh and greater than 45cm dbh (30-45, >45) produced negative coefficients in the model as did the distance to an understory tree. Coefficients and odds ratios of each contributing variable to the whole model can be found in Table 1-4.

CANCLOS was not significant (p > 0.25) at the univariate level for adult males therefore I could not add this term to allow for comparison. I attempted to add DOVER to the female model to allow comparisons to be drawn between males and females, however the difference in AIC added by this variable was 40.8, indicating levels of support for both models are not similar enough.

Since SLOPEANG was not significant enough to be included (p > 0.25) in the univariate analysis for any of the models, I did not evaluate the effect of SLOPEASP. There was no difference in snake occurrence in natural versus artificial edge type (EDGETYPE) for adult female snakes ($X^2 = 0.14$ p = 0.71) or for adult males ($X^2 = 0$ p = 1.00). General habitat type (GENHAB) selection at the micro scale did not differ significantly ($X^2 = 7.7$ p = 0.1735) for male and female H. platirhinos.

Discussion

Home range

Based on the areas of the MCPs, the average home range size of the 17 radio tracked Eastern Hognose Snakes was 39.43 ± 6.3 ha, which is slightly smaller than what other studies have shown for U.S. populations (Lagory *et al.* 2009, Plummer & Mills 2000). Male home ranges were slightly smaller than female home ranges (Figure 1-3), but not significantly so $(33.3 \pm 11.9 \text{ ha}, 41.99 \pm 7.6 \text{ ha respectively})$. The sample size of males included in this study was small (n = 5) and compared to females; fewer males were followed from early spring through to hibernation. The

estimated home range size may be affected by this discrepancy as MCP size in correlated to the number of data points included in the calculation (Hansteen *et al.* 1997).

The use of larger home range areas by male snakes has been attributed in the past to making periodic long-distance travels during mate-searching (Brito 2003). In this study, long-distance travelling by males to copulate with females was observed in several instances; however, females also made long-distance movements towards a nesting site in mid-June. Adult female snakes located in the St. Williams Conservation Reserve (SWCR) were found using a communal nesting site, some travelling over 1 km from the extent of their respective home ranges. Female H. platirhinos are known to use open sand dune habitat to nest (Cunnington & Cebek 2005). In many cases, suitable nesting habitat was more proximal to some female snakes however they chose to migrate farther to use this communal nest site, thus increasing home range size. Because females congregate at this nesting site on SWCR, male snakes may have the advantage of intercepting them as they arrive thus minimizing the need for male locomotion. So if while mate searching, males created any bias towards larger MCPs, it was likely balanced by female migration towards the communal nest site. When I examined the core area of habitat use by snakes using a 50% kernel, very little difference is seen between females and males (6.04) and 5.64 ha, respectively). This confirms that both sexes have similar habitat range needs for the majority of their seasonal activity.

Hierarchical habitat selection

It is evident that Eastern Hognose Snakes use their habitat nonrandomly at both the micro- and macro-habitat scale. Snakes selected certain habitat types in disproportionate frequency to their availability within the landscape. *H. platirhinos* were found using open canopy environments like sand dunes, young tree plantations, and human altered habitat more frequently than denser canopy forests (Table 1-2). Sand dunes appear to be exceptionally important for female snakes as they rely on areas with sandy soils and as much solar radiation as possible to incubate deposited eggs throughout the summer months. Preference for tree nurseries/plantations and altered habitat (Table 1-2) is likely shown because they provide greatest opportunities for basking within edge habitat where some canopy cover allows light penetration while structures for concealment are also present. All habitat types tested were used at a greater frequency than expected from their availability with the exception of cropland, which was avoided by male and female snakes. Although the MANOVA indicated that male and female snakes select home range habitat differently, the compositional analysis for the female population produced essentially the same ranking of habitat types. As the male population size was too small to analyze, I can only speculate that the variation in the model arose from male selection.

Within their home range, Eastern Hognose Snakes showed preference for different types of habitat than at the general landscape scale. Human altered habitat like roads and residential areas were ranked ahead of forests, sand dunes, and plantations. Agricultural land ranked third in the matrix, which can be attributed to

the use of edge habitat along cropped fields rather than actual use of the fields themselves. Sand dunes are used by female *H. platirhinos* during the short nesting period in June, thus it is logical that they ranked lower at the scale of home range. While wetlands appear as a moderate contributor to home range habitat, snakes rarely used them. So while I see selection for sand dune habitat at the macro-scale, snakes appear to incorporate more human altered landscape into their activity pattern throughout their home ranges. Coniferous forest is also used more frequently at the home range scale. In the SWCR property eastern white and red pine (*Pinus strobaus* and *P. resinosa* respectively) were planted in the 1930's in uniform stands (Draper et al. 2002) and for the most part, remain intact presently. When a mature tree falls from wind or disease in this type of forest community a large gap is left in the canopy whereas in a mixed forest the canopy is made up of trees of varying heights so the impact of one fallen tree is not as drastic. In this study, I found that snakes took advantage of these sites where downed white pines created an opening in the forest canopy.

Microhabitat site selection by Eastern Hognose Snakes was evident as well in this study with both sexes showing preference for locations with woody debris, suspended foliage like saplings, raspberries, ferns, and graminoids as well as a higher number of logs (Table 1-3). Mature trees with a diameter of >30 cm were significant contributors to the regression model as negative coefficients meaning sites with mature trees were avoided. Distance to an understory tree was a negative predictor as well in that the probability of a used site increased as the distance to an understory tree decreased (Table 1-4). So sites were frequently located in close

proximity to saplings and small trees. When evaluated alone, female snakes also chose sites covered with more woody debris and foliage, fewer overstory trees, but surprisingly higher canopy cover. Nesting sites were not included in this analysis, therefore perhaps after oviposition has occurred thermoregulation through basking becomes less important. Blouin-Demers & Weatherhead (2001) found that female rat snakes maintained a higher body temperature and exploited their thermal environments more frequently prior to oviposition. Another explanation may be that following the nesting season the ambient temperature remains consistently high in this region of Ontario so females may not need to bask in direct sun. Male micro-sites were similar to females with the addition of distance to an overstory tree as a negative predictor of site use. So while sites used by males had fewer overstory trees, snakes were more likely to bask, rest or hide close to one. General habitat type including forest, field, edge and sand dunes was recorded at each characterized micro-site, however no preference was detected at this scale. Future studies should perhaps evaluate the use of edge habitat at the home range scale using GIS mapping technology.

Thermoregulation dictates the activity patterns and behaviour of most ectotherms (Mullin & Seigel 2009), however the importance of habitat quality may be different between the sexes. Eastern Hognose snakes are oviparous and mature females can develop up to 42 eggs (Peet-Paré 2010). Vitellogenesis can take several weeks during which time the female metabolic rate must be elevated (Ladyman *et al.* 2003, Birchard *et al.* 1984) and so choosing high quality habitat for thermoregulation during this period is especially important. This trend towards

increasing thermoregulatory opportunities through seasonal adjustments in habitat use is evident in Eastern Hognose Snakes at both 2^{nd} and 3rd orders of selection.

Management implications

My study has shown that Eastern Hognose Snakes rely on open sand barren habitat for nesting activities in early summer (mid-June). These findings are consistent with other studies on *H. platirhinos* in the northeastern United States (Lagory *et al.* 2009, Plummer & Mills 1996, Munyer 1967). I also found that female snakes exhibited breeding philopatry where individuals returned to nest at the exact location used the previous season. This indicates that identifying and protecting the nesting grounds of any population of Eastern Hognose Snakes could be a critical step in the recovery of this species. Species with high site fidelity are less adaptable to habitat loss and degradation (Warkentin & Hernández 1996) therefore particular attention should be given to conservation of open fields and sand barrens.

Habitat management and conservation of forest reserves are the most successful ways to help declining populations survive and recover (Taylor *et al.* 2011). However, conservation of sand dune habitat, whether inland or adjacent to bodies of water, is difficult as it is often used for human recreation. In the case of the SWCR property, the use of all-terrain-vehicles was prevalent throughout the summer in the open field/dune region where nesting takes place. Reproductive individuals are often the key for population viability (Shine & Bonnet 2000) and are already at enough risk from travelling without the addition of ATVs driving through

nesting sites. Non-conforming land-use, especially in sensitive areas, does not bode well for adult survival, nest-site viability or juvenile recruitment rates of this threatened species and conservation measures should be put in place to ensure these activities do not jeopardize the future of *H. platirhinos*.

Another concern regarding nesting grounds is that secondary succession eventually turns old-field habitat into mature forest. Fire succession plays a large role in maintaining the vegetative community of old-field habitat. When early successive species are exposed to fire, succession can be arrested and smaller shrubs and grasses replace later successional tree species like *Quercus* (Santana *et al.* 2010). If succession continues, old field and inland sand dune habitat is eventually taken over by mature forest. Prescribed burns have recently gained attention as a management technique for maintaining old-field habitat and eliminating non-native plants (Boyles & Aubrey 2006, Hancock 2009). This technique could prove to be useful in the future for creating and maintaining nesting grounds for Eastern Hognose Snakes.

Following nesting activities, I found that snakes migrate towards human altered habitats like tree plantations, residential yards, and the edges of agricultural fields. Human persecution has been identified as a major threat facing Eastern Hognose Snakes mainly because their defensive display can be quite alarming (Seburn 2009). Therefore, if snakes are encountering humans while traversing agricultural fields and using woodpiles and residential yards to bask, the most powerful conservation tool I can imagine is citizen awareness. Education should

focus on ecology rather than the sensational aspects of snake behaviour and should target rural area schools, migrant agricultural workers, and landowners.

Table 1-1. Habitat variables assessed at used and random locations in the microhabitat analysis of 17 Eastern Hognose Snakes (*Heterodon platirhinos*) followed by radio-telemetry in the Long Point Region of Ontario, Canada.

	Radius	
Variable	(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
%SUSFOLI	1	Coverage (%) by living suspended foliage within plot
%WOODY	1	Coverage (%) by woody debris within plot
SLOPEANG	1	Angle of the slope (° elevation)
SLOPEASP	1	Aspect of the slope (compass °)
#LOGS	5	Number of logs ≥7.5 ch dbh within plot
#SUSSNAG	5	Number of suspended snag within plot
<7.5	5	Number of trees with <7.5cm dbh in plot
7.5-15	10	Number of trees ≥7.5 and <15 cm dbh in plot
15-30	10	Number of trees ≥15 and <30 cm dbh in plot
30-45	10	Number of trees ≥30 and <45 cm dbh in plot
>45	10	Number of trees ≥45 cm dbh in plot
CLOSELOG	30	Closest distance to a log (≥7.5 cm dbh) in plot
DOVER	30	Closest distance to an overstory tree (≥7.5 cm dbh) in plot
DUNDER	30	Closest distance to an understory tree (<7.5 cm dbh) in plot
GENHAB	30	Description of general habitat surrounding plot
HCANOPY	30	Average height of canopy (m) within plot
DISTEGE	100	Distance to edge habitat (m) from plot
EDGETYPE	100	Type of edge transition (natural or artificial)
%CANCLOS	45	Coverage (%) of arboreal canopy within a 45 degree cone

Table 1-2. Matrices of Student's *t* values and *p* values comparing habitat types (CROP, CONIF, DECID, ALTER, MIXED, PLANTA, SAND) for 17 Eastern Hognose Snakes (*Heterodon platirhinos*) in the Long Point Region of Ontario, Canada.

	CROP		CONIF		DECID		ALTER		MIXED		PLANTA		SAND		
	t	p	t	p	t	p	t	p	t	p	t	p	t	p	RANK
CROP			-1.80	0.09	-3.29	0.01*	-4.35	0.001*	-3.19	0.01*	-3.25	0.01*	-5.57	<0.0001*	7
CONIF					-1.30	0.22	-3.06	0.01*	-1.75	0.10	-1.45	0.17	-3.03	0.01*	6
DECID							-1.80	0.10	-0.53	0.60	-0.34	0.74	-2.70	0.02*	5
ALTER									1.93	0.07	1.65	0.12	-1.27	0.22	2
MIXED											0.13	0.90	-2.51	0.02*	3
PLANTA													-3.30	0.01*	4
SAND															1

Table 1-3. Matched-pairs logistic regression models explaining microhabitat use by Eastern Hognose Snakes (*Heterodon platirhinos*) in the Long Point Region of Ontario, Canada. Models with the lowest Akaike Information Criterion (AIC) scores and highest Akaike weights (ω) have greater support. Number of model parameters (k) is also listed.

Model	k	AIC	ΔΑΙC	ω
X.WOODY, X.SUSFOLI	2	122.5921	16.3723	0.0001
X.WOODY, X.SUSFOLI, X30.45	3	106.2198	13.2872	0.0005
X.WOODY, X.SUSFOLI, X30.45, X.45	4	92.9326	0.3570	0.3152
X.WOODY, X.SUSFOLI, X30.45, X.45, DUNDER	5	92.5756	0.4075	0.3074
X.WOODY, X.SUSFOLI, X30.45, X.45, DUNDER, X.LOGS	6	92.1681	0.0000	0.3768

Table 1-4. Coefficients ± SE and odds ratios for matched-pairs logistic regression model explaining microhabitat use by Eastern Hognose Snakes in the Long Point Region of Ontario, Canada.

Variable	Coefficient	SE	Increase	Odds	95% C.I.
				Ratio	
X.WOODY	0.0426	± 0.022	1%	1.0435	(0.999, 1.09)
X.SUSFOLI	0.0466	± 0.013	1%	1.0477	(1.02, 1.07)
X.30.45	-0.3837	± 0.104	1 tree	0.6813	(0.56, 0.84)
X.45	-0.7749	± 0.238	1 tree	0.4608	(0.29, 0.74)
DUNDER	-0.0008	± 0.001	0.01 cm	0.9992	(0.998, 1.00)
X.LOGS	0.1222	± 0.789	1 log	1.1299	(0.97, 1.32)

^{* 95%} C.I. from odds ratios

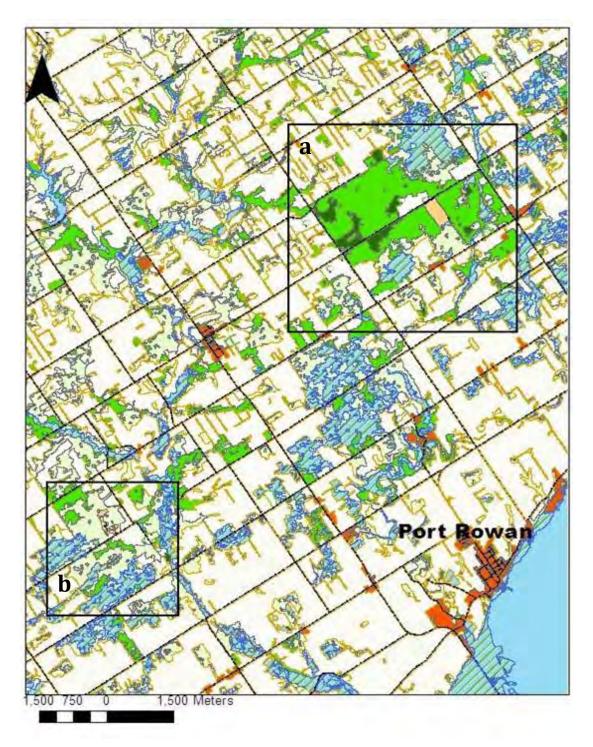


Figure 1-1. Eastern Hognose Snake study sites near Port Rowan, Ontario, Canada. a) St. Williams Conservation Reserve b) Walsingham – Big Creek Corridor.

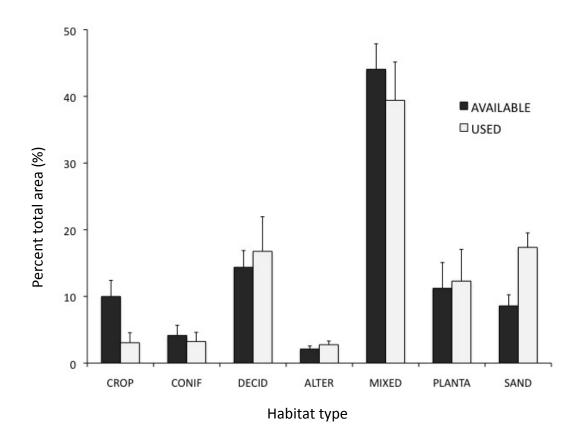


Figure 1-2. Percent total area (mean ± SE) of the 7 macrohabitat types within the 95% kernel home ranges (used) and the available habitat for all Eastern Hognose Snakes (*Heterodon platirhinos*) tracked in the Long Point region of Ontario, Canada. N = 17.

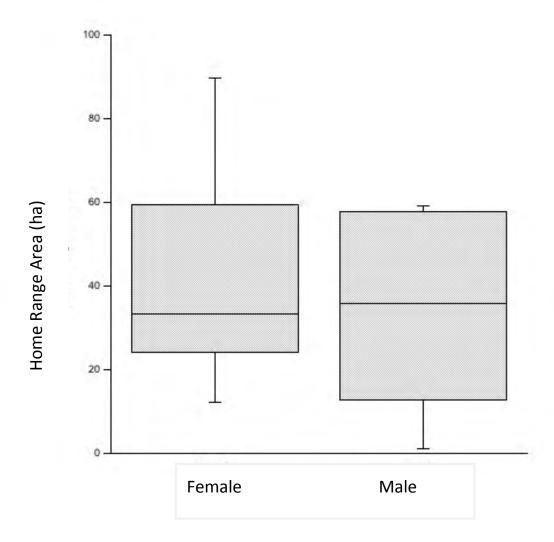


Figure 1-3. Total home range size (ha) measured with minimum convex polygons for each sex of Eastern Hognose Snakes (*H. platirhinos*) tracked in the Long Point Region of Ontario, Canada. No significant difference exists between means (N = 12, 5).

CHAPTER 2

Do Eastern Hognose Snakes (*Heterodon platirhinos*) avoid crossing roads?

Abstract

Human infrastructures like road networks negatively affect the natural environment. Roads can directly impact animal populations by increasing the risk of mortality; however, a more subtle ecological effect may lie in the way roads impede gene flow by creating barriers to animal movement. I investigated the impact of a road network, containing both paved and unpaved surfaces, on the movements of Eastern Hognose Snakes (Heterodon platirhinos) in the Long Point region of Ontario, Canada by radio-tracking 25 adult snakes over 2 years. I tested the hypothesis that roads constrain movements because snakes avoid crossing them. Overall, the road network did not impede snake movements. When examined separately, however, I showed that snakes avoided crossing paved roads while they crossed sand roads readily. Male and female snakes crossed roads at the same frequency. While the risk of road mortality is reduced by road avoidance, such avoidance of paved roads may contribute to the genetic isolation and further decline of this species-at-risk.

Introduction

Threats posed by development on biodiversity

With the increasing rate of human population growth comes added pressure on the natural environment. Increasing urban sprawl means denser road networks and their associated traffic. There is a growing body of evidence suggesting that road infrastructure may have a negative impact on wildlife and is a driving force behind the global loss of biodiversity (Tremblay & St. Clair 2011; Benítez-López et

al. 2010; Fahrig 2003). Studies on many groups of animals, including large and small mammals (Long 2010; Zurcher et al. 2010; Ford 2008), herptiles (Row et al. 2007; Vos & Chardon 1998; Findlay & Houlahan 1997), birds (Reijnen et al. 1995; Kociolek et al. 2011), and invertebrates (Seibert & Conover 1991) have demonstrated the range of detrimental effects roads have on wildlife. Amphibians exist in lower densities when in proximity to road networks (Findlay & Houlahan 1997, Vos & Chardon 1998). Reijen et al. (1995) suggested that road noise decreases bird densities along roadside habitat. Mammals and reptiles have been found to alter movement and migration patterns to avoid crossing roads (Zurcher et al. 2010), but also suffer from road mortality where crossing occurs (Row et al. 2007). Row et al. (2007) showed that road mortality was sufficient to explain the observed population decline in a local population of large snakes. When roads cause changes in animal movement patterns, they may restrict access to necessary resources like water, breeding and nesting grounds as well as food supply. While these challenges may pose immediate negative consequences to animals, the barrier effect roads have on gene flow may be subtler. If roads are avoided, or if individuals are unable to cross roads and survive, animal populations may become genetically isolated resulting in low genetic diversity and inbreeding depression (Holderegger 2010). Due to their vagility, but low velocity, reptiles and amphibians face the highest risk of road mortality of any terrestrial animal group (Andrews 2005; Ashley 1996).

Isolation and loss of gene flow are major threats facing species-at-risk in North America. What is of greatest concern for at-risk populations, however, is the rapid rate of habitat loss and fragmentation occurring as a result of urban and

agricultural development (Fahrig 1997). Road networks decrease the patch-size of intact habitat. When animals are forced to use smaller, sub-optimal patches of habitat, resources may become scarce and predator pressure high (Arnold et al. 1993; Šálek et al. 2010).

Road mortality

Males and females often have divergent ecological needs, thus movement patterns should reflect theses differences in behaviour (e.g., Kuykendall & Keller 2011; Sillero 2008; Blouin-Demers & Weatherhead 2001). If different patterns of movement exist, then rates of road mortality may be different between the sexes. Many studies have focused on quantifying road mortality and the effects it plays on population viability, but few have focussed on intraspecific variation in road mortality (but see Row et al. 2007; Rees et al. 2009). If one sex is more susceptible to road mortality, demographics of the population can change quickly and lead to declines. Road mortality was found to be highest amongst male Massasauga Rattlesnakes (Sistrurus catenatus) compared to females and mortalities were concentrated in August during the mate-searching period (Shepard et al. 2008). Row et al. (2007) showed that road mortality of female Ratsnakes (Elaphe obsoleta) had a much more severe impact on the population than that of males. It is therefore imperative that we measure the impact road networks have on the spatial ecology of animals, especially species that are threatened, so that the risk of road mortality and genetic isolation may be mitigated.

Objectives

The goal of this study was to test the hypothesis that movements of Eastern Hognose Snakes (Heterodon platirhinos), a species classified as threatened by the Committee on the Status of Endangered Wildlife in Canada, are constrained because the snakes avoid crossing roads. I used movement data from a 2-year radiotelemetry study to determine whether roads are crossed less often than expected by chance by males and females. I also examined whether paved roads were avoided more than unpaved roads.

Methods

Study area and species

H. platirhinos is a large-bodied snake (up to 125 cm in total length) that reaches maturity at 2-4 years (Michener 1989). Average lifespan in the wild is estimated at 12 years (Platt 1969) and females produce up to 42 eggs per clutch (Peet-Paré 2010). I conducted this study from May 2009 to October 2010 in the Long Point Region of Ontario, Canada (Latitude: 42° 42' 07" N Longitude: 80° 28' 08" W). The study area consisted of 2 separate properties ca. 1035 ha and 500 ha comprised mainly of oak savannah, mixed forest, old-field, shallow wetlands, and pine stands with sandy soils. The first property, the St. Williams Conservation Reserve, is bisected by 2 sand roads and is bordered by paved roads on 3 sides (Fig. 2-1). The second property (Fig. 2-2), the Walsingham – Big Creek corridor, is a combination of private lands, Nature Conservancy of Canada and Long Point Region

Conservation Authority lands, and is also bisected by several sand and paved roads. Speed limits along these roads range from 50 - 80 km/h and the annual average daily traffic (AADT) volume for surrounding roads ranges from 6,350-10,350 vehicles/day (MTO 2007).

I captured individual snakes opportunistically throughout the active season. I surgically implanted radio-transmitters in a total of 25 adult snakes (17 females & 8 males) and tracked them for periods ranging from a several weeks to 2 years. Several snakes were lost to predation and so I used the movement patterns of 17 snakes (12 females & 5 males) that were tracked over a complete active season in my analyses. Individuals with radio-transmitters were located every 5 days during peak activity season (1 May to 31 August). At each location, the Universal Transverse Mercator (UTM) coordinates were recorded using a GPSmap76Cx portable GPS unit (Garmin International Inc., Olathe, KS) at an accuracy of < 4 m.

Road avoidance

I estimated road avoidance for each individual by comparing the actual number of road crossings made by the individual to the number of road crossings it would have made given a random course. I generated 100 'random walk' movement paths for each individual snake (Klingenbock et al., 2000; Row et al. 2007) using the Animal Movement Extension (Hooge & Hooge 2001) in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California). Each random movement course started in the same location as the real snake to which it was paired and had the

same chronological series of distances moved, but I randomized the bearing at which the pathway turned at each location (Fig. 2-3). This set of 100 random pathways, along with the true snake movement paths, were then intersected with the entire road network. I also intersected the paved and unpaved road network separately to see if substrate plays a role in road avoidance. I compared road avoidance between the sexes by subtracting the observed crossing value from the mean expected value for each individual and performing a non-parametric ANOVA (Wilcoxon signed-rank test) on the differences. To test for individual road avoidance, I created a distribution of road crossings for each individual from the 'random walk' pathways (expected crossings) and compared the actual pathway (observed crossings) to this distribution. I deemed a snake to avoid roads significantly when its observed number of crossings was less than the 5% percentile of the distribution of expected crossings. The number of snakes who significantly avoided roads was tallied and I used a sign-test to determine whether roads were avoided significantly at the population level.

Results

There was no significant difference in the degree of road avoidance between the sexes (R2 = 0.002, F1,15 = 0.02, p = 0.88) therefore I pooled the sexes for further analyses. Hognose snakes crossed roads an average of 1.65 ± 0.51 times per season (maximum number of crossings = 6), whereas snakes moving randomly traversed roads an average of 1.88 ± 0.21 times per season (maximum number of crossings =

10) (Fig. 2-3). Overall the 17 snakes did not significantly avoid crossing roads (Fig. 2-4) (sign test p > 0.1), but the number of observed crossings was significantly less than the number of expected crossings for 11 out of 17 snakes. When I repeated the analysis separately for paved and unpaved roads, I found that snakes did not avoid crossing unpaved roads (sign test p > 0.1; the number of observed crossings was significantly less than the number of expected crossings for 10 out of 17 snakes), but they did avoid crossing paved roads (sign test p = 0.0001: the number of observed crossings was significantly less than the number of expected crossings for 16 out of 17 snakes).

Discussion

Several studies have documented road avoidance in reptiles (Klingenbock et al. 2000, Koenig et al. 2001, Andrews et al. 2005), but others have found that large snakes may not avoid crossing roads (Row et al. 2007). Eastern Hognose Snakes did not avoid crossing unpaved roads, but they did avoid crossing paved roads. This suggests that, unsurprisingly, all roads are not equal in their effect on wildlife movement. I anticipated a difference between the frequency of male and female road crossings due to their differences in reproductive ecology. The observed rate of overall crossings was, however, similar for the sexes but small sample sizes (especially of males) reduced my ability to detect a difference if it indeed existed. Paved roads are avoided by hognose snakes, which should reduce road mortality but increase population isolation, while unpaved roads are crossed readily, which

should increase road mortality but decrease population isolation if a sufficient number of snakes succeed in traversing the road without being killed by a car. If few snakes make it across unpaved roads alive or if paved roads are avoided, hognose snakes may be susceptible to the potential barrier effect created by roads, leading to a reduction in gene flow across populations.

The distribution of Eastern Hognose Snakes is divided into two distinct groups in Canada: the southwestern Ontario population and the Wasaga-Oak Ridge Moraine-Peterborough corridor (Oldham & Weller 2000). It is currently unknown whether any genetic flow exists between these populations, but given the extensive road network and my results on road avoidance it appears unlikely. Wildlife underpasses have been shown to reduce overall mortalities along highways especially when fencing is also present (McCollister & van Manen 2010). As hognose do appear to avoid paved road crossings, populations may benefit from the construction of wildlife culverts and aquatic underpasses.

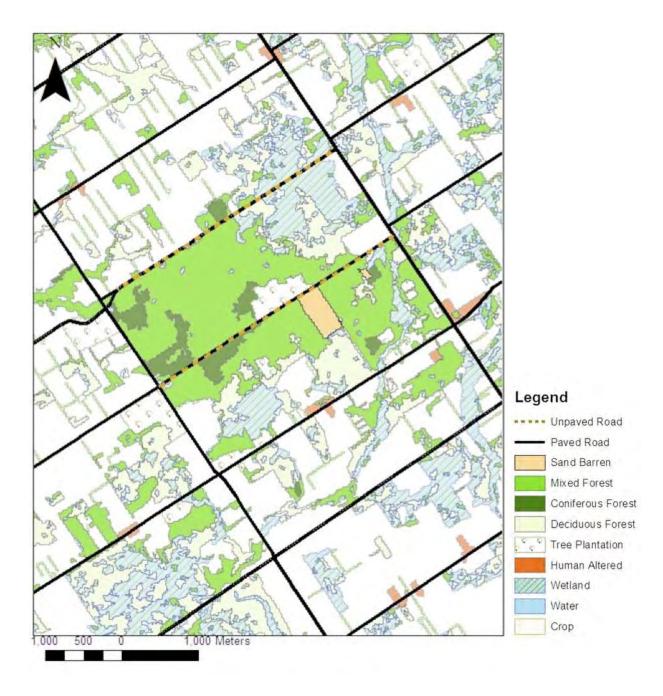


Figure 2-1. Land classification and road network surrounding the St. Williams Conservation Reserve, Long Point Region, ON, Canada.

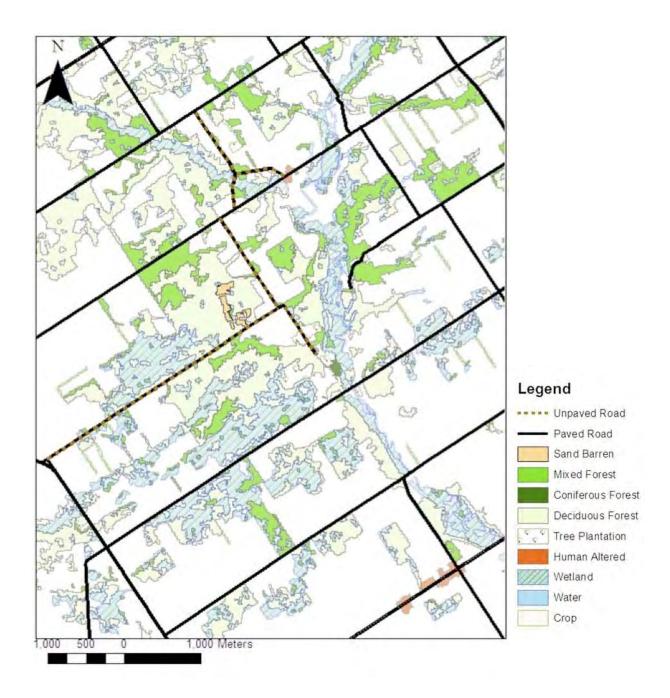


Figure 2-2. Land classification and road network surrounding the Walsingham – Big Creek Corridor, Long Point Region, ON, Canada.

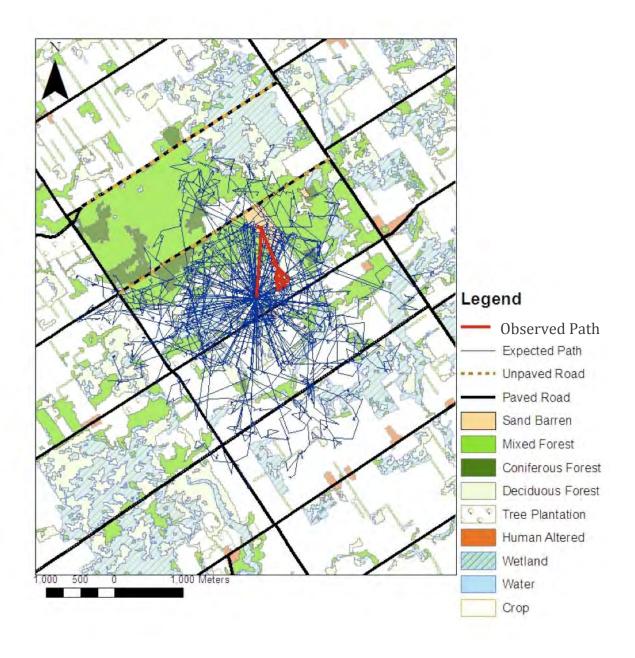


Figure 2-3. Observed and expected pathways across paved and unpaved roads of one Eastern Hognose Snake (*Heterodon platirhinos*) in the St. Williams Conservation Reserve.

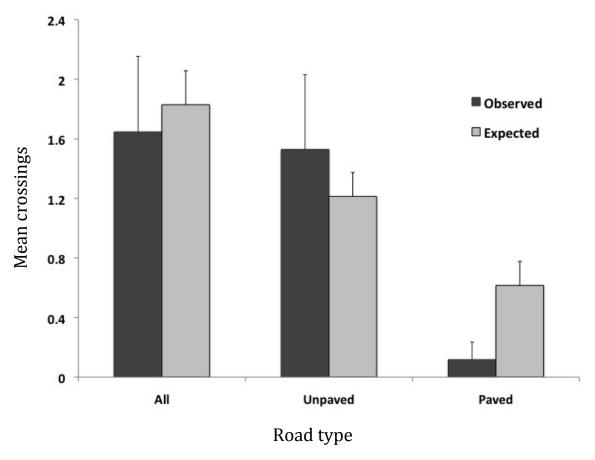


Figure 2-4. Mean (± SE) observed and expected road crossings over all surfaces, unpaved and paved roads by Eastern Hognose Snakes (*Heterodon platirhinos*) in the Long Point Region of Ontario, Canada (N = 17).

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