Multi-Scale Patterns of Eastern Milksnake (*Lampropeltis triangulum)* Habitat Selection and

Behavioural Responses to Habitat Fragmentation

by

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Authors Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

The decline of species with specific habitat needs can be attributed to human caused habitat destruction and fragmentation. This is particularly concerning for reptiles, as they are often unable to adapt to modified landscapes. The eastern milksnake (*Lampropeltis triangulum)* represents the rare case of a species at risk that has persisted both in disturbed and undisturbed landscapes throughout its historic Canadian range. However, a lack of contemporary occurrence data makes it difficult to assess the impact of perceived threats on the species, or devise effective conservation strategies. Here, I aim to quantify milksnake habitat selection and potential behavioural adaptation in response to human development at multiple spatial scales. Specifically, I address the questions 1) Do milksnakes modify behaviours (home range size, movement rates) in response to human modified landscapes? 2) Which habitats are milksnakes selecting for at the home range scale, and within the home range, which microhabitat features are selected for? And 3) How does landscape scale habitat fragmentation impact milksnake distribution? I used radio telemetry to track 17 individuals between 2015 and 2017 in Rouge National Urban Park, and used a large scale coverboard survey to generate occurrence records across the Credit Valley and Toronto Region Conservation Authority Management Areas. Using this data, I analyzed movement rates, assessed the degree of road avoidance, determined home range sizes, and compared these metrics to a natural site. I then analyzed home range scale habitat selection, and determined which microhabitats features are selected for within home ranges. Using occurrence data, I determined best predicted landscape scale habitat for milksnakes, and compared this to a generalist species. Results indicate that milksnakes are modifying behaviours in urban landscapes, as they have significantly higher movement rates and avoid road crossings. Milksnakes are also avoiding human modified landcover types (urban area and agriculture) at all scales. At the home range and

microhabitat scales, milksnakes are selecting a variety of open habitats with abundant cover, while selection at the landscape scale favours large habitat patches. In order to conserve snake populations, I recommend that conservation of large natural areas and the establishment of corridors connecting them are prioritized.

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1 General Introduction

Pressures on wildlife in the form of human-driven habitat loss and fragmentation are the leading causes of contemporary extinction events globally (Fahrig, 1997; Gill, Sutherland, & Watkinson, 1996; Hoekstra, Boucher, Ricketts, & Roberts, 2005; Krauss et al., 2010). Wildlife species demonstrate incredible variation in their ability to tolerate human disturbances, as species respond to different types of disturbances at different scales (Bender, Contreras, & Fahrig, 1998; Cagnolo, Valladares, Salvo, Cabido, & Zak, 2009). Species that thrive in these fragmented landscapes typically utilize a combination of small habitat patches and surrounding developed areas (Gill et al., 1996). Alternatively, species with specific habitat needs and several species at risk often experience further decline and displacement due to anthropogenic disturbances, which may result in a low likelihood of long term persistence on the landscape (Ewers & Didham, 2006; Kerr & Deguise, 2004). Understanding how species respond to anthropogenic pressures is therefore essential to predict global biodiversity trends and develop effective conservation strategies. However, responses to habitat fragmentation and loss are not linear, meaning responses to these threats occur along a gradient, with different species being impacted at varying scales both spatially and temporally.

The eastern milksnake *(Lampropeltis triangulum)* represents the rare case of a species at risk that has persisted in both disturbed and undisturbed regions throughout its historic range. Recognized threats for milksnakes include road or rail mortality, habitat loss from urban development, intensive agriculture, and persecution due to misidentification as a poisonous species (COSEWIC, 2014). These recognized threats are concerning throughout the species Canadian range due to the ongoing and intensive development.

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Current knowledge of milksnake habitat selection is limited to a study on a large piece of intact habitat (Row & Blouin-Demers, 2006b, 2006c). This leaves a knowledge gap regarding the species ecology in disturbed area, as it remains uncertain how disturbance influences available habitat, behavioural ecology, and habitat selection. To fill this knowledge gap, this thesis systematically quantifies milksnake habitat selection and behavioural modification at multiple spatial scales in a developed region.

2 Review of the Literature

2.1 A Brief History of Niche Theory

Niche theory involves the study and formal definition of the mechanisms driving wildlife occupancy of environmental and geographic space. Scientists have long attempted to explain these mechanisms, which has led to the development of competing definitions of niche and many sub theories (Schnieder & Willig, 2005). Niche theory was originally developed at two separate sub-theories focused on place of a species (Grinnell, 1917) and role of a species (Elton, 1927) in explaining distribution (Schnieder & Willig, 2005; Soberón, 2007). Grinellean niche considers a species occupancy of geographic space a direct response to a narrow range of environmental conditions, defined by non-interactive environmental variables on coarse scales (Grinnell, 1917, Soberón, 2007). Eltonian niche considers competition for resources between species at local scales as the primary driver of occupancy of environmental space (Elton, 1927; Soberón, 2007).

In an attempt to clarify these terms, Hutchinson (1957) proposed that a species niche can be defined quantitatively as an n-dimensional hypervolume of factors influencing persistence of a given species (Hutchinson, 1957; Schnieder & Willig, 2005). Fundamental niche of a species is represented by all of the points in this n-dimensional space that meet the species requirements, theoretically allowing it to exist (Hutchinson, 1957). The inherent complexity of ecological systems and biotic interactions do not necessarily allow access to all points within this space. Realized niche is then the n-dimensional space that a species can occupy based on competition with interacting species, and dispersal ability (Hutchinson, 1957; Schnieder & Willig, 2005).

The development of more advanced quantitative methods in ecology has since allowed Hutchinson's niche concept to be challenged statistically (P. H. Harvey, Colwell, Silvertown, & May, 1983; Schnieder & Willig, 2005; Simberloff, 1978). Simberloff (1978) used a null model to

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test whether colonization based on species interactions differs from random chance, finding that the null model preformed quite well with the caveat that vertebrate distribution remains influenced by diffuse competition (P. H. Harvey et al., 1983). Despite the performance of thoughtfully parameterized null models, a number of competing hypotheses and models exist to explain wildlife occurrence patterns (P. H. Harvey et al., 1983).

There has since been robust development in ecological modelling and the ability to address many competing hypotheses and predict species distributions across landscapes, though clarity is often lacking as to whether these models explain distribution or niche (Elith & Leathwick, 2009; Raudsepp-Hearne & Peterson, 2016; Soberón, 2007). Models explaining niche account for interactions between species, while models explaining distribution are based on environmental data (Elith & Leathwick, 2009).To clarify what a given model type explains, it is important to note the distinction between mechanistic models predicting niche and correlative models predicting distribution (Elith & Leathwick, 2009; Kearney & Porter, 2009; Soberón, 2007). Mechanistic models include information regarding links between organisms and their environment (such as behavioural, morphological, and physical traits) (Kearney & Porter, 2009). As a consequence, mechanistic models are able to provide outputs which indirectly represent many processes (Kearney & Porter, 2009). However, the data regarding mechanistic links between organisms and their environments is only available for well studied taxa (Kearney & Porter, 2009; Soberón, 2007). Correlative models are more widely applicable probability based models related to broad scale habitat parameters and requiring decidedly less detailed species data (Elith & Leathwick, 2009). The term correlative models is applied to describe many distribution modelling approaches also referred to as: bioclimatic models, climate envelopes, ecological niche models, species distribution models, range maps, and resource selection functions (Elith & Leathwick, 2009). The

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lack of information regarding biotic interactions in correlative models raises the question of whether they examine realized or fundamental niche. Guisan and Zimmermann (2000) argue that models based on field data depict the realized niche, as occurrence observations are obtained in the form of occupied animal locations which are based on biotic interaction with other species.

2.2 Defining Habitat and Associated Terms

Models predicting a species occurrence based on habitat are subject to the assumption that if an animal uses a habitat type disproportionately to its availability, then that habitat is biologically relevant (Aebischer, Robertson, & Kenward, 1993; Johnson, 1980). This assumption is widely accepted, but the definitions of habitat and related terms vary throughout the literature (Hall, Krausman, & Morrison, 1997). For consistency in this study, we adopt definitions for habitat and associated terms based reviews of previous use in the literature (Krausman, 1999; Lele, Merrill, Keim, & Boyce, 2013). Habitat is defined as the resources and conditions present in an area that lead to occupancy by an organism (Krausman, 1999). These resources include factors (such as food, cover, water) that are required for a species survival and reproduction, including seasonally used migration and dispersal corridors (Krausman, 1999; Leopold, 1933). For studies that include distribution modelling approaches, the distinction must also be made between resource units and resource types (Lele et al., 2013). Resource units are items available for consumption distributed through the landscape, or pixels imposed on a landscape to represent habitat (Lele et al., 2013). In this study, I use resource units in the form of pixels imposed on the landscape to represent habitat types, and as a consequence the terms habitat type and resource unit are used somewhat interchangeably. If multiple resource units have the same attributes, they are considered the same resource type. (Lele et al., 2013).

Habitat use is the way these resources are used (for forage, cover, nesting, or a variety of other life history traits), though a given resource is not always used exclusively for one life history

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trait (Krausman, 1999). Likewise, resource units are considered used if they subject to investment by an animal for perceived benefit (Buskirk & Millspaugh, 2006; Lele et al., 2013). Habitat use is subject to seasonal variation based on life history traits and dispersal (Elith & Leathwick, 2009; Krausman, 1999; Peterson, 2006). For example, an animals seasonal breeding sites, hibernation sites, forage sites, and corridors connecting them all represent used habitat. Without data that encompasses multiple seasons, it may not be possible to identify habitat use associated with all important life history traits.

Habitat use does not necessarily imply habitat selection as an animal may use one habitat or resource unit as a means of accessing another (Krausman, 1999). Habitat selection refers to the use of a habitat by an animal if that habitat it is encountered (Lele et al., 2013). Habitat selection is relatively intuitive to understand as a binary term, with an encountered habitat considered used or unused (Boyce, Vernier, Nielsen, & Schmiegelow, 2002; Lele et al., 2013). Probability of selection is then the probability that a given habitat type will be used if encountered, based solely on the habitat type and its ability to satisfy a life history trait (Lele et al., 2013). Probability of use refers to a single instance of use in a given habitat type and is limited by whether that habitat can be accessed (Lele et al., 2013). If a habitat type is selected for but is inaccessible, then it will have a low probability of use (Lele et al., 2013).

Habitat selection is a hierarchical process which has been suggested to occur at four distinct spatial scales (Johnson, 1980). First order selection is the physical or geographic range of a species, which dictates second order selection of a home range (Johnson, 1980). Third order selection is the use of various habitat types and sites within the home range, while fourth order selection involves the procurement of food items or other benefit from those sites (Johnson, 1980).

These orders of habitat selection are relatively intuitive to understand, and assessing habitat selection at an appropriate spatial scale has long been considered important in quantifying wildlife habitat, however, all habitat at a given scale is not equally accessible to an individual (Johnson, 1980). While it is clear that appropriate scales must also be selected, a species' ability to access habitat at a given scale must be considered. This requires researchers to develop an understanding of species' ability to move through a given landscape. Ability to access suitable habitat patches is often limited in urban landscapes.

2.3   Urban Ecology – An Emerging Discipline

Urban ecology is a relatively new sub-discipline of ecology that is generally thought to have begun in the 1970's (McDonnell, 2011; McDonnell & Pickett, 1993). The need to consider urban ecology as a distinct sub-discipline emerged from the recognition that human development fundamentally changes ecosystems by fragmenting and removing habitat (Deelstra, 1988; McDonnell, 2011; Niemela, 2000). These processes are especially intensive in urban areas relative to rural areas, as natural landscapes are often removed rather than altered. Urban ecology has then emerged partially out of necessity, as rapid human population growth has left few ecosystems unaltered. Early definitions of urban ecology focused on the integration of: 1) natural sciences, 2) engineering/urban planning, and 3) social sciences (Deelstra, 1988; McDonnell, 2011). However, more recent work has stated that social sciences and natural sciences within urban ecology should be considered as distinct fields of study, with the social component focussing in human health as it related to the environment and the natural component focusing on biological processes (Niemela, 2000). These fields fall under the umbrella of urban ecology as long as they occur in urban areas where 85% of the population lives is non-rural (Niemela, 2000; Rebele, 1994).

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Ecological studies in urban areas typically focus on the ability of wildlife to access habitat, patch characteristics, or invasion by invasive species (Niemela, 2000; Rebele, 1994). In urban areas, the ability of wildlife to access suitable habitat is negatively impacted by high intensity roads, dense development, and a lack of corridors (Gill et al., 1996; McDonnell & Pickett, 1993; McKinney, 2006). Additionally, decreases in patch size and increases in disturbance limit the ability of wildlife to access suitable habitat and persist in urban landscapes (Hagen et al., 2012). The theory of island biogeography has historically been applied to understand patch characteristics in urban landscapes, by treating isolated urban habitat patches in the same way as islands (Davis & Glick, 1978; MacArthur & Wilson, 1967). Fragmented patch characteristics alter species composition to favour invasive species and generalists (Hagen et al., 2012; Randa & Yunger, 2006). Species richness is often high in urban ecosystems due to a variety of edges and microhabitats, but this does not necessarily indicate a healthy system as the function that the historic state of the system may not be replicated (McDonnell, 2011; Niemela, 2000; Rebele, 1994). Recent work has shown that urbanization and the impacts on wildlife occur along a gradient from rural to urban (Randa & Yunger, 2006). Still, wildlife species are limited by patch size and their ability to access suitable habitat in urban areas.

2.4   Herpetofauna and Susceptibility to Human Impacts

Herpetofauna are especially susceptible to the negative impacts of habitat loss and fragmentation (Gibbons et al., 2000). They are a relatively slow moving group of species often with specific habitat needs (Gibbons et al., 2000; Reading et al., 2010). Though reptiles and amphibians are both considered herpetofauna, they are morphologically and behaviourally distinct (Gibbons et al., 2000; Reading et al., 2010). Reptiles generally have much larger home ranges and higher movement rates than amphibians, which makes them more susceptible to negative impacts

of habitat fragmentation (Gibbons et al., 2000). This thesis is concerned with snakes, but it is worth noting that amphibians face many of the same pressures and are subject to the same trends of decline (Gibbons et al., 2000)

In recent years, snake populations have experienced a marked decline globally across habitat types and species (Mullin & Seigel, 2009; Reading et al., 2010). It is possible that global population decline has been occurring for much longer, but with few long term snake studies on which population can be assessed, this remains an assumption (Reading et al., 2010). Snakes are often top predators so a decline in their numbers can have serious consequences for ecosystems (Reading et al, 2010).

The potential impact of habitat loss on snakes is relatively simple to understand. If important habitat or habitat features (such as hibernation sites) are removed from a landscape, the animal will not persist if it cannot access these features elsewhere (Mullin & Seigel, 2009; Reading et al., 2010). To contrast this, the effects of habitat fragmentation are often subtle. Perhaps the most obvious of these impacts is road mortality, which is higher in fragmented areas (Row, Blouin-Demers, & Weatherhead, 2007). Fragmentation by roads and development can also lead to altered home ranges, as some species are unwilling or unable these features to access former home range areas (Klingenbock, Osterwalder, & Shine, 2000). In the long term, these factors can lead to behavioural changes, reducing gene flow between population clusters (Clark, Brown, Stechert, & Zamudio, 2010; Klingenbock et al., 2000; Shepard, Kuhns, Dreslik, & Phillips, 2008). When habitat patches are not suitable large to sustain populations, regional extirpation or extinction can occur (Germaine & Wakeling, 2001; Rudolph, Burgdorf, Conner, & Schaefer, 1999).

2.5   Study Species – The Eastern Milksnake

The eastern milksnake *(Lampropeltis triangulum)* represents the rare case of a relatively long lived species at risk snake that has persisted in both disturbed and undisturbed areas throughout its range. The species range extends throughout eastern North America, reaching its northern limits in Ontario and southern Quebec's Great Lakes/St. Lawrence and Carolinian regions (COSEWIC, 2014; Ruane, Bryson, Pyron, & Burbrink, 2014). Despite historic occurrence through large parts of Canada's most populated regions, little contemporary information is available on the species in this area, with most of the existing knowledge coming from one study in a natural landscape (COSEWIC, 2014; Row & Blouin-Demers, 2006b, 2006c). Limited information on population size and distribution has contributed to the species national listing as Special Concern (COSEWIC, 2014). Current knowledge on the extent of Canada's milksnake population comes primarily from occurrence records submitted to the Natural Heritage Information Centre (NHIC). These records show that developed regions are dominated by historic records with relatively few observations post 2000. This is evident around Toronto, Ontario, as populations persist throughout the region but are thought to have been in decline for over 30 years (COSEWIC, 2014). This decline has not been confirmed, as no studies on population size or formal survey for the species has taken place prior to 2011.

Milksnakes are historically associated with low intensity agricultural areas, even owing their name to occurrence in cattle barns (COSEWIC, 2014; Lentini, Yannuzzi, Phillips, & Johnson, 2015). Human features in these low intensity agricultural landscapes and small mammal borrows are important habitat features for milksnakes for a variety of life history traits (such as feeding, hibernation, shelter). Abundance of small mammals, the primary food source of adult milksnakes, is typically high in these habitats (COSEWIC, 2014; Lentini et al., 2015). Barns and foundations also provide readily accessible and highly suitable hibernation sites (COSEWIC, 2014; Lentini et

al., 2015). The preservation of these human made habitat features is then important to conserve the species (Lentini et al., 2015). Milksnakes are also a very cryptic species, rarely basking in the open and preferring to thermoregulate using ambient heat on the underside of exposed objects or vegetation (COSEWIC, 2014).

Milksnakes are regarded as a generalist species throughout their range based on their occurrence in many habitat types. I argue that the Canadian population should be considered specialists, and that previous conclusions about habitat specialization have been made at an inappropriate spatial scale. As the Canadian population of milksnakes is at the species northern range limit, thermal quality is much lower than elsewhere in the species range. Snakes occurring in high thermal quality habitat are able to bask indiscriminately, which allows for use of a broad range of habitat types (Ralph Gibson & Bruce Falls, 1979). At their northern range limits, snakes are known to select habitat based on thermal quality (Goulet, Litvaitis, & Marchand, 2015; Row & Blouin-Demers, 2006b, 2006c). Row & Blouin-Demers (2006b, 2006c) found milksnakes to have strong association with fields and open habitats in close proximity to forest edges. The use of open habitats by milksnakes is consistent across seasons (Row & Blouin-Demers, 2006c) In these thermally challenging habitats, milksnakes alter seasonal basking behaviour for thermal benefit rather than altering habitat selection, spending longer periods of time basking as temperature decreases (Row & Blouin-Demers, 2006b). It is clear that current knowledge demonstrates that milksnakes in Canada select few high quality thermal quality habitats within their home range. In this thesis, I consider milksnakes to be specialists of fields and open habitats near forest edges, based on the availability of high quality thermal sites and potential prey in these areas.

2.6   Thesis Outline and Research Questions

This thesis aims to quantify milksnake habitat selection and potential behavioural adaptation in response to human development at multiple spatial scales by answering the following questions: 1) Do milksnakes modify behaviours (home range size, movement rates) in response to human modified landscapes?; 2) Which habitats are milksnakes selecting for at the home range scale and within the home range, which microhabitat features are selected for?; And 3) How does landscape scale habitat fragmentation impact milksnakes distribution?

Questions 1 and 2 are addressed in chapter 3, where I compare movement rates and home range size between a disturbed and natural site to determine the degree to which habitat loss and fragmentation can influence them. Additionally, I quantify second and third order habitat selection within the disturbed site to understand which landcover types and micro-habitat features are selected for in a developed area. Overall this chapter provides an understanding of behavioural adaptations and habitat selection by milksnakes in response to disturbance.

Question 3 is addressed in Chapter 4 where I compare predicted landscape scale distribution of milksnakes to a generalist species. In this chapter, I analyze habitat selection across scales for both species at the landscape scale and investigate the strength of selection and avoidance for multiple, biologically-relevant, landcover types. I then develop spatially-explicit predictions of the relative probability of occupancy for each species and created an overlay of best predicted habitat to understand the potential for multi-species conservation prioritization. Overall, this chapter provides a deeper understanding of the ways in which landscape scale habitat fragmentation potentially impacts milksnakes.

2.7   Study Area

Southern Ontario represents an excellent case to understand species responses to varying human-caused pressures (Kerr & Deguise, 2004). The most significant threats to wildlife from habitat destruction and fragmentation can be observed in the southern Great Lakes region, which contains approximately 25% of the country's population (Kanter, 2005). The region is also home to 130 nationally listed species at risk and 500 provincially rare species; while a mere 2% of the land area is subject to formal protection (Kanter, 2005). Many of these rare species reach their northern range limits in this region, which compounds the effects of habitat loss and fragmentation and leads to many species at risk listing decisions.

I use three different study areas throughout this thesis: 1) Rouge National Urban Park (RNUP), 2) Queens University Biology Station (QUBS) and 3) the combined management areas of the Credit Valley Conservation Authority (CVC) and Toronto Region Conservation Authority (TRCA) referred to as the Greater Toronto Area (GTA). For this reason, different study areas will be described further detail in the corresponding chapters.

3 Habitat Selection and Behavioural Modifications by Milksnakes in Response to Habitat Fragmentation

3.1 Introduction

Human-caused habitat destruction and fragmentation of intact habitat patches are among the greatest threats to global biodiversity (Fahrig 2007, Gill et al 1996, Hoekstra et al 2005, Krauss et al 2010). The ability of wildlife populations to persist with increasing levels of these threats is varied and often dictated by the size of habitat patches and their proximity to other intact patches (Atwood, 2006; McKinney, 2006). Patch characteristics can vary depending on land use, and moving along a rural to urban gradient, habitat patches generally become smaller and more isolated, favoring generalist species and leading to the extirpation of those with specific habitat needs (McKinney, 2006; Pickett et al., 2001, Gill et al., 1996). It is projected that 60% of the global population will soon live in urban areas, and with this increase the size of urban areas are expanding at a rapid rate (Seto, Guneralp, & Hutyra, 2012). The majority of this growth is expected to take place in areas where existing habitat already faces direct stressors from humans, placing further pressure on wildlife populations as fragmentation increases (Faaborg, Brittingham, Donovan, & Blake, 1993; Seto et al., 2012).

Roads are one of the most prevalent causes of fragmentation in urban environments (Forman & Alexander, 1998; Mader, 1984) and they have been directly linked to an array of impacts on wildlife populations across many taxa. These impacts include increased mortality (Row, Blouin-Demers, & Weatherhead, 2007), altered home ranges (Klingenbock et al., 2000), and changes in movement patterns or behaviour (Forman & Alexander, 1998; Shepard et al., 2008). In the long term, these factors lead to changes in population size and demography (specifically sex ratios), reduced gene flow (Aresco, 2005; Clark et al., 2010), and potentially regional extirpation or extinction (Germaine & Wakeling, 2001; Rudolph et al., 1999). In urbanizing areas, former

rural roads are often widened and see an increase in traffic. These changes amplify negative effects as higher traffic intensity and increasing road width are known to further deter vertebrate crossings and increase mortality (Robson & Blouin-Demers, 2013; Richard Shine, Lemaster, Wall, Langkilde, & Mason, 2004). As a consequence, species with large home ranges and high site fidelity are unable, or must risk vehicle collisions, to access core home range areas (Forman & Alexander, 1998).

As a relatively slow moving group of species, snakes may be at a heightened risk to the negative effects of roads (Shepard et al., 2008). The impacts of road mortality in particular are an issue for this group potentially due to the fact that many snake species use roads for thermoregulation in areas with diel temperature variation (Richard Shine et al., 2004). In urban areas the lack of sufficient resources and potential mates in small habitat patches often necessitates crossings (Ettling, Aghasyan, Aghasyan, & Parker, 2016). Increased road related mortality can have significant long term effects on snake population sizes at both the site and landscape levels (Congdon, Dunham, & van Loben Sels, 1994; Rudolph et al., 1999) particularly in northern climates, where individuals have slow growth and long life-spans (Row et al., 2007).

In addition to the direct population impacts associated with mortality, roads also impact snake behaviour. Snakes typically take the shortest path possible (Shine et al., 2004) or avoid crossing paved roads altogether (Robson & Blouin-Demers, 2013; Shepard et al., 2008). This avoidance can lead to alterations in home range and movement relative to populations not disturbed by development. As a consequence, roads can add to the effects of habitat loss and act as significant barriers to genetic transfer between snake populations, which can lead to isolation of subpopulations (Row, Blouin-Demers, & Lougheed, 2012). However, landscapes featuring corridors of moderate quality habitat and several small, suitable habitat patches have been shown

to have a positive influence on overall population connectivity (Row et al., 2012; Row, Blouin-Demers, & Lougheed, 2010).

Given many potential threats of urbanization and habitat loss to snake populations there is an increasing need to better understand snake ecology in disturbed areas. The eastern milksnake *(Lampropeltis triangulum)* is one species whose life history is closely connected with human altered environments (COSEWIC, 2014). They are commonly found in rural areas, where hibernation and feeding sites such as building foundations and mammal borrows are abundant (COSEWIC, 2014). Milksnakes use a variety of open habitats and forest edges that can be abundant in rural areas (COSEWIC, 2014; Row & Blouin-Demers, 2006c). Despite this association, occurrence records from the most developed portion of their range appear to lack contemporary locations. Habitat loss, fragmentation, and road mortality led to a federal listing as a species of special concern. With many parts of their range now facing pressure from urbanization, snake populations are also threatened. However, current information on milksnake behaviour and habitat selection is derived from rural and natural areas, with their responses to anthropogenically dominated landscapes yet to be quantified.

Here, my overall objective is to quantify the habitat selection and movement patterns for milksnakes in a developed region bordering a major urban center. Specifically, I compare movement rates and home range size from the urban site (Rouge National Park, herein RNUP) to individuals in a more natural landscape (Queens University Biology Station, herein QUBS) to determine the degree to which habitat loss and fragmentation can influence movement. Because of the large number of roads at the disturbed sites I will also analyze road crossings to quantify whether individuals actively avoid roads. I expect higher movement rates and larger home ranges at RNUP as they relate to the search for food and mates in a fragmented landscape (Ettling et al.,

2016). However, significant avoidance of roads may act as a constraint, leading to smaller home range sizes (Clark et al., 2010). I also quantify second and third order habitat selection within the disturbed site to understand which landcover types and micro-habitat features are most significant in urbanizing areas. I expect a broad range of natural habitats to be used relative to previous studies, while intensive agriculture and urban areas will be avoided. I also expect cover objects, to be important in individual site selection, but expect the number of these objects to be limited on the landscape. Overall my results provide a deeper understanding of behavioural adaptations of milksnakes in response to disturbance.

3.2 Methods

3.2.1 Study Area

Rouge National Urban Park (RNUP) is a newly established 79.1km^2 reserve located in the Rouge Valley directly east of the City of Toronto, Canada along the Rouge River and Little Rouge Creek watersheds (Figure 1). The landscape is a mix of agricultural land, natural areas, and cultural heritage sites connecting the Oak Ridges Moraine to Lake Ontario and bordered by heavily urbanized areas to the east and west. The natural areas within Rouge Valley are composed primarily of secondary growth forest interspersed with meadow, along with lowland swamps. Several of these natural areas are restored pastureland and cropland in an early successional state, bordered by hedgerows of mature trees. Cultural heritage sites in Rouge Valley such as stone cottages, foreclosed farmhouses, and barn foundations remain largely intact. Rouge Valley is bisected by 2 major highways, several multi-lane roadways, and two sets of high traffic rail lines. Although all locations are not directly within RNUP park boundaries, hereafter I refer to all individuals tracked in and around this region as being within the RNUP study site.

The Queens University Biology Station (QUBS) study area is a 24km^2 reserve located approximately 100km south of Ottawa, Ontario (Row & Blouin-Demers, 2006c)(Figure 1). The study area is characterized by an array of natural secondary growth deciduous forest, rocky outcroppings, and old fields. QUBS has far less fragmentation, with no adjacent development and only one non-major road bisecting the study area (for additional information see Row & Blouin-Demers, 2006c; Row, Blouin-Demers, & Weatherhead, 2007).
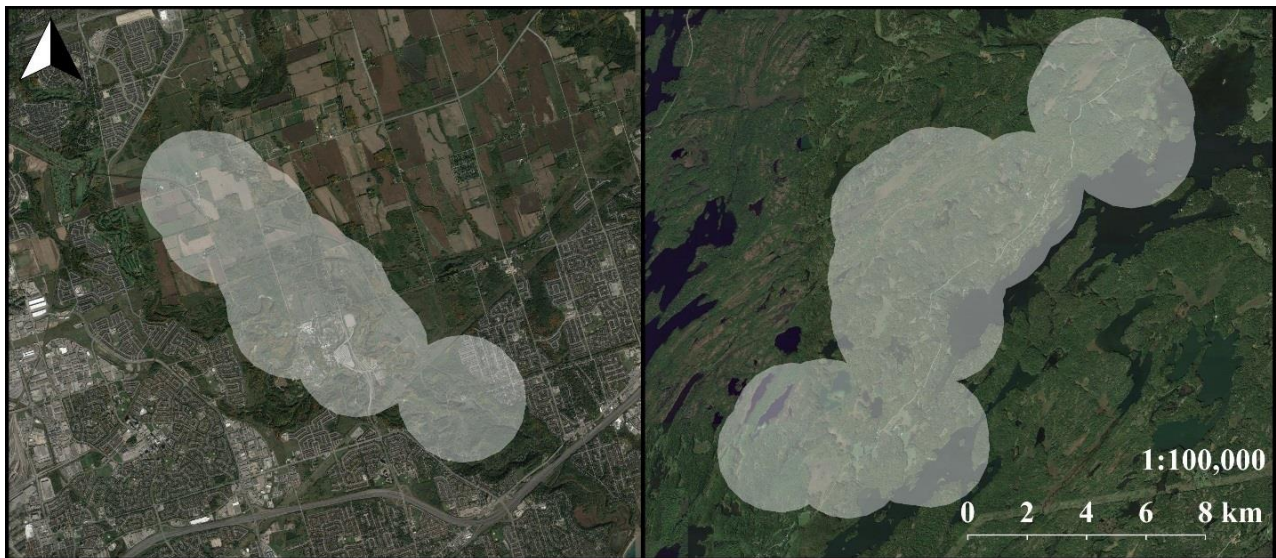
Figure 1. Maps of Rouge National Urban Park and Queens University Biology Station study areas created by placing 1km radial buffers around all occurrence locations generated using radio telemetry. Contrasting land used surrounding the study areas are apparent here.

Individuals were captured at QUBS (by Dr. Jeff Row) during the 2003-2004 seasons using incidental captures of individuals at black ratsnake (*Pantherophis spoloides)* hibernation sites that also had a high abundance of milksnakes, opportunistic captures and by placing and checking artificial cover objects that attract individuals (herein cover board). At RNUP individuals were captured primarily through a large-scale cover board survey and opportunistically during the 2015 -2016 seasons. We surveyed approximately 160 cover boards placed between 2010 and 2015 (board size 1.2m x 0.8m) at 14 sites throughout RNUP. Cover boards survey represent a low

maintenance means of monitoring and capturing herpetofauna that places minimal risk of injury or stress on the animal (Grant et al., 1991).

At QUBS, 30 individuals with implanted with radio transmitters (produced by Holohil Systems, Carp, Ontario, Canada) constituting <5% of the snakes' mass. At RNUP, programmable radio-transmitters (produced by Sigma Eight, Aurora, Ontario, Canada) were implanted in 17 non-gravid individuals large enough so that transmitter weight constituted <4% of the snakes mass (Moore & Gillingham, 2006). At both sites I allowed a 24-hour recovery period in captivity and then returned individuals to their capture location and relocated them 2-3 times weekly during the active season (release date – early September), with additional observations recorded bi-weekly through October (Row & Blouin-Demers, 2006b). For each observation, we recorded the GPS location of the individual (Garmin International, Kansas City, KA), its position, general behaviour, and habitat characteristics.

3.2.2 Difference in Home Range Size Between Sites

I calculated home range size for all individuals tracked for a full active season (May – September) at both sites (Ettling et al., 2016; Moore & Gillingham, 2006; Vanek, Wasko, College, Hall, & Hartford, 2017) using 95 % Minimum Convex Polygons (MCP's) (Boyle, Lourenço, Da Silva, & Smith, 2009; Byer, Smith, & Seigel, 2017; Calenge, 2006; Moore & Gillingham, 2006; Row & Blouin-Demers, 2006a, 2006b; Sutton, Wang, Schweitzer, & McClure, 2017). For individuals that were not tracked for a full season, I determined whether the entire home range was utilized by plotting home range size against number of relocations (Boyle et al., 2009; Rowy & Blouin-Demers, 2006c). If home range size reached an asymptote, it was determined that the entire home range was used and the individual was included in the analysis (Row & Blouin-Demers, 2006c). Gender was included as a factor in home range analysis due to increased movement rates

for males during reproduction, and gravid females were removed from the analysis as we only tracked 3 such individuals (Sutton, et al., 2017). A multi-factor ANOVA and Tukey HSD test were used to assess differences in home range size between sexes and sites.

3.2.3   Differences in Movement Rates Between Sites

I analyzed movement rates of all individuals during peak activity season at both sites (May-September) (Row et al., 2007; Sutton et al., 2017). For each individual, I calculated daily movement rates (DMR) and distance-per-move (DPM) (Sutton et al., 2017). DMR was calculated by averaging observed travel distances over the days between relocations. DPM was calculated by averaging sequential distances for all relocations showing movement from the previous location (Diffendorfer, Rochester, Fisher, & Brown, 2005). Per-move values eliminated consecutive relocations where the individual remained in the same location. Average DPM excluded all values <5m based on the maximum error of the GPS prior to calculating sequential distances (Diffendorfer et al., 2005). For both movement rate metrics, I modelled the influence of sex and region using linear mixed effects models, in which individual was included as a random intercept to control for individual variation.

3.2.4   Road Avoidance in A Fragmented Landscape

I tested for road avoidance by individuals at RNUP. This analysis was not conducted at QUBS because there was only 1 road with much lower traffic rates and few individuals in the proximity of the road. Beginning at the first location, I generated random bearings independently based on a random number between 0 and 360 and simulated a movement matching the distance of the observed movement (Klingenbock et al., 2000; Robson & Blouin-Demers, 2013; Row et al., 2007). I repeated this process at each newly generated random location, resulting in a series of random movement paths that matched observed paths in distance (Klingenbock et al., 2000; Robson & Blouin-Demers, 2013; Row et al., 2007). I then took mean number of road crossings

from each individual for both observed and random movement paths and assessed the differences using a paired t-test (Row et al., 2007). Significantly higher road crossings for random paths would suggest active avoidance of road crossings.

3.2.5 Habitat Selection at the Home Range Scale

I developed a large-scale GIS landcover data layer using a variety of sources and comprised of 7 landcover types. Data containing classified natural landscapes (forest, meadow, successional, wetland) RNUP were obtained from the Toronto Region Conservation Authority (TRCA) and confirmed through aerial photography (Table 1). Urban and agricultural land cover was obtained through the Government of Canada's Open data portal in the form of Agriculture and Agri-Food Canada's (AAFC) Ontario wide 2014 Crop Inventory at $30m^2$ resolution (Agriculture and Agri-Food Canada, 2014). AAFC data informed the creation of polygons to ensure borders matched TRCA landcover borders. The roads layer used for crossing analysis was also included as a landscape covariate I then derived density of each landcover type within moving windows with a radius of 15 m.

To assess home range selection at RNUP, I compared landcover class densities at used versus available locations at the home range scale (Aebischer et al., 1993). Available habit was defined within radial plots centered at the hibernation site of each individual. The radius used for each individual was set to the maximum distance travelled from the hibernaculum (Row & Blouin-Demers, 2006c). Random points matching the number of observed locations were established within radial plots for each individual. Habitat classes at each used and random location were then extracted from the moving window transformations. The size of the moving window (15m) represents the size of plots used for analysing individual scale-habitat selection (section 3.2.6). I examined mean values of habitat type for both used and absence locations for each individual, to

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ensure there were no outliers for multiple habitat covariates (Figure 15). I analysed the potential

difference in habitat type between observed and random locations using generalized linear mixed

effects model with individual included as a random intercept. An exhaustive list of candidate

models was generated and ranked based on ΔAIC values. All models producing ΔAIC <2 were

considered as potentially contributing to differences in selection of used versus unused habitat

types (Arnold, 2010).

Table 1. Landcover layers used in modelling home range scale habitat selection by eastern milksnakes in Rouge National Park and the justification for including layers.

Layer	Source (year)	Original pixel(m)	Resampled pixel(m)	Description	Justification
Forest	TRCA (2015)	Spatial Polygons	3 x 3	All ELC classifications of forest.	Core component of natural areas.
Meadow	TRCA (2015)	Spatial Polygons	3 x 3	Meadow habitat not employed as pasture or fallow field	Old fields and road edges often restored as meadow habitat
Successional	TRCA (2015)	Spatial Polygons	3 x 3	Habitats transitioning from meadow to forest. Often planted restoration projects on old fields	Represents restored meadows in a later state, restoration sites with planted trees, and transition areas.
Wetland	TRCA (2015)	Spatial Polygons	3 x 3	Marsh and swamp including open water contained within wetlands.	Core component of natural areas.
Agriculture	AAFC (2014)	30 x 30	3 x 3	Remote sensing derived, including all cover and cash crops.	North end of study area bordered by agriculture.
Urban	AAFC (2014)	30 x 30	3 x 3	Remote sensing derived, including all densities of urban development	South, east, and west ends of study area bordered by urban area.
Roads	DMTI (2016)	Spatial lines	3 x 3	All paved and unpaved roads	Many major roads bisect study area.

3.2.6 Habitat Selection at the Individual Location

I examined third order selection of habitat components within home ranges at RNUP

(Johnson, 1980) using fine scale habitat data of structural variables collected using paired used-

available habitat plots. I surveyed every other telemetry location and established random available

locations within a distance accessible to the individual. (Row & Blouin-Demers, 2006c).

Beginning at the used location, we spun a compass to select a random bearing, then rolled a 20-sided dice, multiplying the outcome by 10 to select a random number of steps to walk to a theoretically available location (Row & Blouin-Demers, 2006c). Habitat plots were completed when it was ensured through telemetry that the individual had moved to a new location (~2-14 days after collection of the occurrence record). I developed pair logistic regression models, effective for comparing presence absence plots of wildlife, (Compton, Rhymer, & McCollough, 2002; Row & Blouin-Demers, 2006c) which considered a suite of biologically relevant variables, both collected in the field and created post survey (Table 2).

Table 2. Names and definitions of variables used in modelling habitat selection at individual locations in Rouge National Urban Park.

Name	Definition
Vobstruct	Height and density of surrounding vegetation: used a Robel pole to determine the visual minimum and maximum height of vegetation and averaged these values
Dedge	Distance to forest edge (> 10 clustered trees with adjoining canopy and DBH >10cm) to a maximum of 15m
Canopy	Percent canopy cover measured using a densitometer
Dcov	Distance to nearest potential cover object (minimum 50cmx50cm)
Ncov	Number of potential cover objects with 15 m of the location.
Sumcov	The total area of cover objects available within 15m of the location. Derived area from length and width measurements of individual objects and totaled their areas.
Vegheight	The average vegetation height within a 1m radial plot of the exact location. Three measurements were taken randomly and averaged.
DTree	Distance to the nearest tree having a diameter at breast height >10cm, and occurring within 15m of the location

I examined correlation between all predictors and evaluated those producing an unacceptable level of correlation ($r > 0.6$) with univariate models. Models were ranked based on ΔAIC and the variables producing the lowest values were retained. All variables were scaled to center their means on 0, and an exhaustive list of candidate models was generated. I ranked candidate models based on ΔAIC values, considering those with ΔAIC <2 as potentially contributing to the

difference between presence and absence points (Arnold, 2010). Because variables were scaled, lager coefficient values represented a larger effect on habitat selection.

3.3 Results

We collected 1001 observations of 30 individuals at QUBS over the 2003 and 2004 seasons, and 453 locations of 17 individuals in RNUP throughout the 2015 and 2016 seasons (Table 3). I compare these two datasets because QUBS has experienced little chance in vegetation structure and habitat availability from data collection to present.

Table 3. Number of individual milksnakes tracked by site and sex, including metrics associated with the number of relocation at Rouge National Urban Park and Queens University Biology Station.

Site	Sex	# of Individuals	# of Relocations		
			Max	Min	Mean
RNUP	*M*	*12*	*39*	*6*	*23.58*
	F	*5*	*42*	*18*	*31.6*
QUBS	*M*	*20*	*51*	*9*	*30.75*
	F	*10*	*52*	*14*	*36.3*

3.3.1 Comparison of Home Range Sizes Between Sites

I excluded 5 individuals from RNUP due to their reproductive status and non-asymptotic home range sizes, resulting in a total of 12 individuals (9 males, 3 females) for the analysis. At QUBS, I excluded 8 individuals due to reproductive status and non-asymptotic home range, leading to a total of 22 available individuals (19 males, 5 females).

Minimum convex polygons at the 95% level varied slightly between sites, with individual home ranges at RNUP having both a smaller mean *(RNUP=7.02±3.02ha, QUBS=11.84±3.26ha)* and reduced range *(RNUP=1.54–23.38ha, QUBS=0.17ha–30.79)* compared to the individuals at QUBS (Figure 2). However, a multi-factor ANOVA found no significant difference in mean home range size between sites *(F=2.36, p=0.14)*. Difference in minimum convex polygon size is more

prevalent in males than females, with males also having larger average home range sizes at both sites. However, a multi-factor ANOVA also found this to be non-significant *(F = 0.56, p = 0.58)*. A Tukey HSD test showed no significant difference within or between sexes across sites *(all p-values >0.70)*.
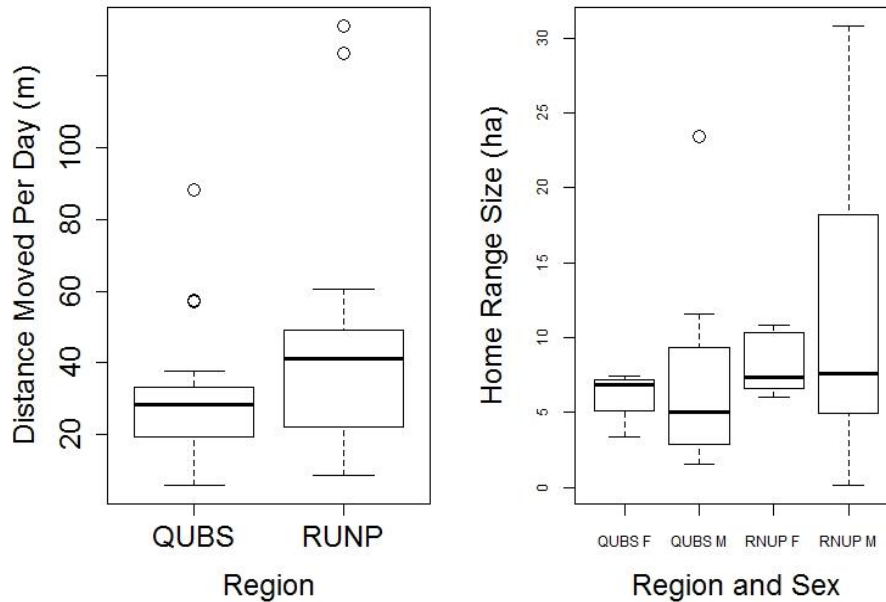
Figure 2. Box plots showing distance moved per day for individuals at Rouge National Urban Park and Queens University Biology Station, and home range size of male and female milksnakes in each study area.

3.3.2 Differences in Movement Rates Between Sites

I derived DMRs for 30 individuals (19 males, 11 females) from QUBS and 17 individuals (12 males, 5 females) from RNUP. Examining movement rates by sex, I found that males at RNUP had smaller mean values than females while males at QUBS had larger mean values than females (Figure 2). These differences between sexes were not statistically significant *(DMR p = 0.64, DPM p = 0.40)*. Examining differences between sites, I found that individuals at RNUP had larger DMR *(RNUP = 53.05 ± 14.83, QUBS = 29.26 ± 5.00)* and distance per movement *(RNUP = 64.56 ±*

15.61, QUBS = 47.54 ±20.22). The distance travelled per movement was significant (p = *0.18, t= 1.37, df = 48.58*), while DMR was significantly higher (*p = 0.01, t=2.69, df = 46.60*) for individuals at RNUP.

3.3.3 Road Avoidance in A Fragmented Landscape

Throughout the study no individuals crossed road, despite many locations being in close proximity to different roads. The mean number of crossings per individual for simulated movements was *3.4 ± 0.7* crossings and ranged from a low of 1.3 to a maximum of 5.1. A paired t-test suggested that the random number of crossings was significantly higher than the number of observed crossings (*t=11.75, df=15, p= <0.001*).

3.3.4 Habitat Selection at the Home Range Scale in Rouge National Urban Park

All 7 habitat covariates had an acceptable level of correlation (p<0.60). Using all covariates, I developed an exhaustive list of models of which 7 contributed significantly to the difference

Figure 3. Standardized coefficients of top model and 97.5% confidence intervals potentially contributing to the differences between used and available locations at the home range scale controlling for individual variation as a random effect.

between used and absence locations (Table 4) Figure 15. Forest, meadow, urban, and agriculture, appear in all top models and negatively influence occurrence to varying degrees (Figure 4).

Table 4. All candidate producing ΔAIC values <2 for milksnake habitat covariates at the home range scale

Model Formula	ΔAIC
Occurrence ~Agriculture+Urban+Forest+Wetland+Road+Meadow	0
Occurrence ~Agriculture+Urban+Forest+Wetland+Road	0.059
Occurrence ~Agriculture+Urban+Forest+Wetland+Successional	0.272
Occurrence ~Agriculture+Urban+Forest+Wetland+Road+Successional	0.298
Occurrence ~Agriculture+Urban+Forest+Wetland	0.443
Occurrence ~Agriculture+Urban+Forest+Wetland+Meadow	1.083
Occurrence ~Agriculture+Urban+Forest+Wetland+Road+Meadow+Successional	1.993

3.3.5 Habitat Selection at the Individual Location in Rouge National Urban Park

I found number of cover objects (Ncov) to have an unacceptable level of correlation with total area of cover (Sumcov) *(r=0.76)* and distance to the nearest cover object (Dcov) *(r=0.72)*, while total area of cover (Sumcov) and distance to the nearest cover object (Dcov) showed an acceptable level of correlation with each other *(r=0.42)*. Distance to the nearest tree (Dtree) was also correlated with canopy cover (Canopy) *(r=0.61)*. Univariate models ranked based on ΔAIC showed little difference between Distance to the nearest tree (Dtree) *(ΔAIC 0.00)* and canopy cover (Canopy) *(ΔAIC 1.48)*. I removed Distance to the nearest tree (Dtree), as prior knowledge on milksnake habitat selection indicates that canopy cover and its associated thermal profile is a better predictor of occurrence that tree cover (Row & Blouin-Demers, 2006b). Additional univariate models examining the remaining 3 correlated variables led to the retention of number of cover objects (Ncov) *(ΔAIC 0.00)* rather than distance to the nearest cover object (Dcov) (*ΔAIC 4.98)* or total area of cover (Sumcov) (*35.02)*. After removing correlated predictors, I used the 5 remaining variables to develop an exhaustive series of 64 candidate models. I found that only the global model produced a ΔAIC <2 (ΔAIC=0.00). All models within ΔAIC <4 from the top model are presented, as these are also thought to be competitive (Arnold, 2010), and assist in illustrating the

importance of individual variables (Table 5). number of cover objects (Ncov) and canopy cover

(Canopy) appear in all 5 models producing a ΔAIC < 4.

Table 5. All candidate producing ΔAIC values <4, and potentially contributing to habitat selection by milksnakes at the exact location.

Model Formula	ΔAIC
Use ∼Ncov+Canopy+Dedge+Vobstruct+Vegheight	0
Use ∼Ncov+Canopy+Vobstruct+Vegheight	2.34
Use ∼Ncov+Canopy+Dedge	2.66
Use ∼Ncov+Canopy+Dedge+Vegheight	3.26
Use ∼Ncov+Canopy+Dedge+Vobstruct	3.51

Examining the top model, all predictors were found to have 97.5% confidence intervals that did

not overlap with zero. The coefficients from the top model show a significant positive relationship

with number of cover objects (Ncov), distance to forest edge (Dedge), and visual obstruction

(Vobstruct) and a significant negative relationship with canopy cover (Canopy) and vegetation
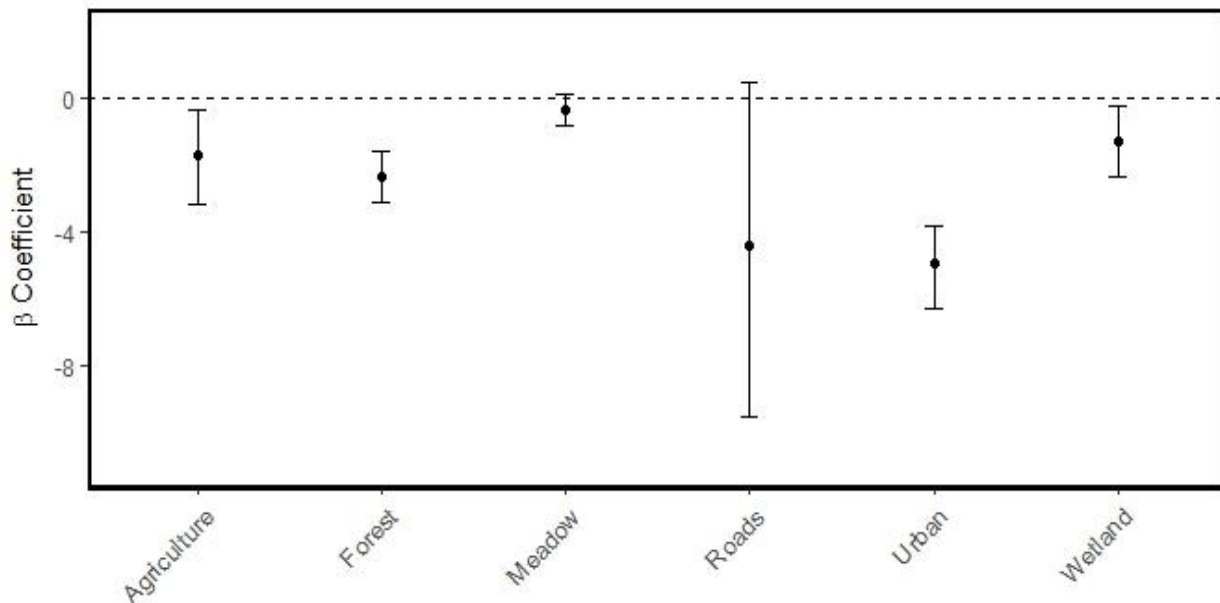
height (Vegheight) (Figure 4).
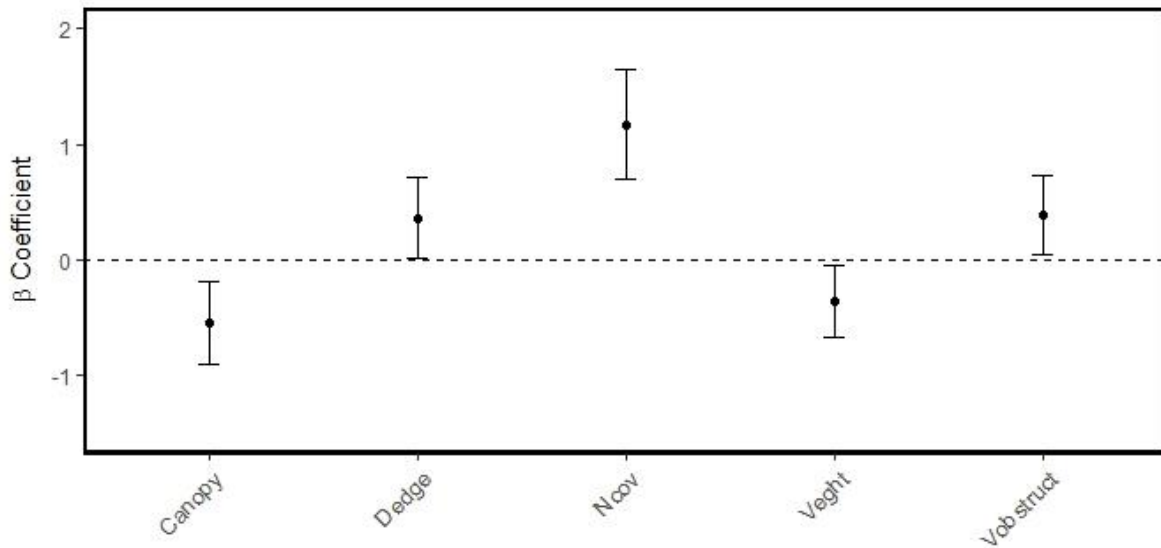
Figure 4. Standardized coefficients of the top model and 97.5% confidence intervals contributing to the difference between used and available locations.

3.4 Discussion

The results highlight the ecology of milksnakes in a developed region and point to potential changes in movement rates and habitat selection patterns in disturbed areas. Along with these changes, milksnakes avoid road crossings despite the close proximity of home ranges and hibernacula to roads. At the home range scale, I found that individuals avoided urban areas, interior forests, and agricultural fields. This was consistent with microhabitat selection where individuals were shown to select for heterogeneous locations (higher surrounding structure, but low at-site vegetation) with low canopy cover. Consistent with milksnakes in more natural areas, individuals selected locations with a high numbers of potential cover objects.

There was no significant difference in home range size between sites, though home ranges at RNUP had a large amount of overlap. These results are consistent with other studies that have found no significant difference in snake home range sizes in response to varying degrees of disturbance (Corey & Doody, 2010; Row et al., 2012). Though fragmentation often constrains snake home range size (Vignoli, Mocaer, Luiselli, & Bologna, 2009), the non-territorial nature of many snake species allows for overlap in home range providing sufficient resources are available (Brattstrom, 1974). Increased home range overlap in fragmented regions been observed in other snake species as a response to constraints on dispersal (Corey & Doody, 2010). The presence of a road directly south of the main hibernaculum is likely constraining the directions which individuals can disperse in RNUP, leading to increased overlap of home ranges relative to QUBS.

Movement rates in snakes are known to change seasonally (Shew, Greene, & Durbian, 2012), vary between sexes, and are influenced by the availability of prey and thermal quality of habitat (Brito, 2003; Friedlaender, 1982; King & Duvall, 1990; Madsen & Shine, 2006). Higher DMR at RNUP cannot be accounted for by seasonal or between-sex variation, as movement rates were analysed over the same duration, and the analysis included similar proportions of male and female

snakes at each site**.** The high amount of overlap between home ranges also points to the search for mates not requiring extensive movement (Brito, 2003). When DMR has been considered in response to anthropogenic influence, it has been found to be both significantly higher (Ettling et al., 2016) and lower (Corey & Doody, 2010) in disturbed areas. However, Corey & Doody's (2010) results are derived from a region where thermal quality is high at both sites and prey abundance is higher at disturbed sites. Alternatively, Ettling et al (2016) found higher prey abundance at disturbed versus natural sites. Low prey abundance in combination with high densities of predators leads to competition for food sources in reptiles (Whitaker & Shine, 2002). Snakes are also known to increase movement rates in response to decreased prey abundance (Mader, 1984; Madsen & Shine, 2006). It is then possible that lower prey densities than QUBS and competition between individuals within overlapping home ranges are leading to increased movement at RNUP. Additionally, QUBS is more forested than RNUP and is known to be a thermally challenging environment as snakes prioritize selection of thermal sites (Row & Blouin-Demers, 2006c). Snakes movement is often constrained by the thermal quality of habitat, with lower movement rates displayed as thermal quality decreases (D. S. Harvey & Weatherhead, 2010) . It is possible that better thermal quality at RNUP then allows for increased movement. However, my data do not include prey abundance or thermal quality of sites in RNUP.

   Larger snake species are more likely to cross roads (Row et al., 2007) and their larger home range sizes can necessitate crossings in urban areas (Bonnet, Naulleau, & Shine, 1999). Here, I found milksnakes avoided road crossings based on a significantly higher number of crossings for random movement paths than observed paths, which is consistent with some other snake species in fragmented areas (Miller et al., 2017; Robson & Blouin-Demers, 2013; Siers, Savidge, & Reed, 2014). In fact, no milksnake in my study ever crossed a road. Milksnakes are a medium sized snake

and home range size did not appear to be constrained, suggesting habitat patch size combined with milksnakes ecology did not necessitate crossings in RNUP. Perhaps if this study were to occur on other sites with smaller patches of habitat, the degree of road avoidance may decrease.

Road avoidance may have long term genetic and population level consequences (Aresco, 2005; Row et al., 2007; Shepard et al., 2008). Size of habitat patches can influence the persistence of snake populations, and unwillingness to cross roads can dramatically decrease available patch size in urban areas (Breininger et al., 2011; Goulet et al., 2015). Further, road avoidance can fragment populations (Clark et al., 2010; Shepard et al., 2008) potentially increasing inbreeding effects (Row et al., 2010). Although it appears that current habitat patches in RNUP are sufficiently large, there are likely impacts of road avoidance on connectivity on a larger regional scale. Ecopassages have been shown to improve genetic connectivity and decrease road mortality in snake species adjacent to high traffic roads (Colley, Lougheed, Otterbein, & Litzgus, 2017). The establishment of corridors connecting even moderate quality habitat can improve population connectivity (Row et al., 2010, 2012), and may be important in improving the likelihood of persistence of milksnakes across this region.

Although milksnakes are traditionally associated with some anthropogenic features (i.e. low intensity farming), I found strong avoidance of urban areas at the home range scale. Agricultural fields were not avoided suggesting a greater tolerance for this habitat, but the overall availability of agricultural fields was low in the study area. Milksnakes also avoid interior forests which was consistent with previous studies that have found milksnakes select forest edges and open habitats (COSEWIC, 2002; Row & Blouin-Demers, 2006c). Interestingly, milksnakes seem to select early successional habitat which made up a significant portion of the study area, and is largely comprised of old fields that have undergone active restoration through wildlife seeding and tree planting.

Our analysis of third order habitat selection (Johnson, 1980) revealed that fine scale habitat structure and heterogeneity of successional habitat likely plays a role in selection for this habitat type. Individuals selected for higher overall vegetation density surrounding used locations, and lower vegetation height at the exact location. This is potentially a trade-off between thermoregulatory benefit and predation risk. Avian species are a significant predator of snakes (Webb & Whiting, 2005) and the increased structure likely provides some visual obstruction. Given that open habitats have greater thermal quality for milksnakes (Row & Blouin-Demers, 2006b) they are likely seeking out locations with greater sun exposure for basking (Charland P.T. Gregory, 1995). In addition to the greater visual obstruction, milksnake choose locations with a higher presence of cover objects which was consistent with natural sites and allows for retreat to cooler sites for thermoregulation (Row & Blouin-Demers, 2006b), and for predator avoidance (Charland P.T. Gregory, 1995). However, the type of cover objects varied between the sites with primarily rock cover objects being replaced with foundations and anthropogenic debris at RNUP (Row & Blouin-Demers, 2006c).

While I have found behavioural modifications, notably road avoidance, by milksnakes in response to development, there is reason for optimism regarding the future of the Rouge Valley population. The newly established Rouge National Urban Park (RNUP), a 78km^2 reserve, largely contains the known milksnake habitat and occurrence locations within the Rouge Valley and represents a positive step towards conserving the species. Within RNUP, disturbance regimes that maintain successional habitats should be promoted. Populations will also benefit from better connection of these existing habitat patches across roads, potentially using ecopassages, to facilitate movement. Furthermore, supplementing restored areas with artificial cover objects will

increase the availability of suitable microhabitats and likely assist milksnake populations long term.

4 Assessing and Comparing Best Predicted Habitat of a Generalist and a Specialist Snake Species Along an Urban Gradient

4.1 Introduction

Habitat loss and fragmentation are the largest global drivers of wildlife population declines and contemporary extinctions (Brook, Sodhi, & Bradshaw, 2008; Fahrig, 1997). These impacts on wildlife occur in all biomes due to human caused land use change driven by rapid human population growth and urban development (Gallant, Klaver, Casper, & Lannoo, 2007; Hagen et al., 2012). The most prevalent large-scale land use changes are clearing and conversion of natural landscapes for agriculture or urban development (Gallant et al., 2007; Recio, Arija, Cabezas-Díaz, & Virgós, 2015). Additionally, the associated transportation networks (e.g., roads) further divides remaining habitat patches (Forman & Alexander, 1998) resulting in decreases in the amount of habitat available on a landscape and the size of habitat patches, and increased patch isolation (Fahrig, 2003). This creates a matrix of habitats divided by barriers that impedes the movement of wildlife (Tucker et al., 2018).

Many native species and communities typically respond poorly to habitat fragmentation. Species with large home ranges are often unable to access former home range areas following human development and the animals are often subject to increased mortality rates or human conflict in modified landscapes. (Congdon et al., 1994; Treves & Karanth, 2003). Specialized species that are dependent on select habitat types or resources, and sessile species, may experience the greatest impacts (Brouat, Chevallier, Meusnier, Noblecourt, & Rasplus, 2004; Devictor, Julliard, & Jiguet, 2008). Additionally, species in fragmented habitats often avoid interaction with humans, leading to isolation from suitable habitat patches (Lees & Peres, 2009). Even when important habitat features are maintained they are functionally lost to the species if they are unwilling or unable to traverse the matrix of unsuitable habitats (McKinney, 2006). Functional

habitat loss leads to genetic isolation between population clusters across multiple taxa (Fedy, Row, & Oyler-McCance, 2017; Row et al., 2010). This can have long term population level effects, increasing the likelihood of regional extinction or extirpation from habitat patches (Crooks et al., 2017).

Generalist species are more capable of adapting to human modified landscapes, as they tend to be mobile, have less specific habitat requirements or are able to modify behaviours, and have high reproductive output (Devictor et al., 2008; Hagen et al., 2012). Impacts of development and habitat fragmentation likely differ between specialist species. It is expected that specialist species select fragmented habitats at larger scales than generalist species, and avoid small highly fragmented patches. To understand which habitats are selected and the scales at which they are selected by generalists and specialists in a fragmented region, comparisons should be made across groups of related species. The Eastern Gartersnake (*Thamnophis sirtalis sirtalis*), a generalist, and Eastern Milksnake (*Lampropeltis triangulum)*, a specialist, are then excellent model species for understanding responses to habitat fragmentation. They have significant range overlap, and are both found in fragmented landscapes (COSEWIC, 2014; Kjoss & Litvaitis, 2001).

Both species use a combination of forest edges and open early successional habitats (Charland P.T. Gregory, 1995; Row & Blouin-Demers, 2006c). Milksnakes are regarded as specialists as they require microhabitats with high thermal quality and an abundance of cover objects for basking (Row & Blouin-Demers, 2006c). Gartersnakes are considered generalists as they bask indiscriminately in a variety of habitats (Charland & Gregory, 1995; Gibson & Falls, 1979). Milksnakes also have larger home ranges (5-10ha) than gartersnakes (~1.5ha)(Kjoss & Litvaitis, 2001, Chapter 2), meaning some fragmented habitat patches may not be suitably large to maintain milksnake populations. Additionally, snakes are known to avoid road crossings (Robson

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& Blouin-Demers, 2013; Shepard et al., 2008, Chapter 3), making them ideal model species for understanding the effects of habitat fragmentation.

To investigate the impact of habitat fragmentation between generalist and specialist species, I focus on milksnake and gartersnake habitats in the heavily fragmented Greater Toronto Area (herein GTA), which have significant range overlaps both historically and currently. I analysed habitat selection across scales for both species at the landscape scale and investigate the strength of selection and avoidance for multiple, biologically-relevant, landcover types. Using this information, I mapped and compared best predicted multi-species habitat. I predicted that the generalist, gartersnakes, would select smaller patches of a variety of natural landcover types, while milksnakes were expected to select larger habitat patches. I predicted greater avoidance of human modified landcover types in milksnakes than gartersnakes. Finally, I developed spatially-explicit predictions of the relative probability of occupancy for each species and created an overlay of best predicted habitat to understand the potential for multi-species conservation prioritization.

4.2 Methods

4.2.1 Study Area

The Greater Toronto Area is Canada's largest metropolitan area with a population of approximately 6 million (Conway & Hackworth, 2007; Vaz & Arsanjani, 2015). It is one of North America's fastest growing urban centers, and is expected to account for 80% of Ontario's population growth until 2030, putting it on track to become Canada's first megacity (>10m inhabitants) (Conway & Hackworth, 2007; Eidelman, 2010; Sahely, Dudding, & Kennedy, 2003; Vaz & Arsanjani, 2015).

The natural areas in the core of Toronto are largely limited to the floodplains and ravines of several rivers (Credit, Humber, Don, Rouge) and creeks that run generally north-south towards

Lake Ontario. The north end of the GTA includes parts of the Ontario Greenbelt, which places formal protection on agricultural and natural lands through established limits on urban growth (Eidelman, 2010). The largest natural areas in the region are to the north and represent secondary growth forest along the Niagara Escarpment and Oak Ridges Moraine. Natural areas in the GTA are highly fragmented by roads and developments (Figure 5). I delineated the study area within the GTA based on the extent of the Toronto Region Conservation Authority (herein TRCA) and Credit Valley Conservation Authority (herein CVC) management areas (Figure 5).
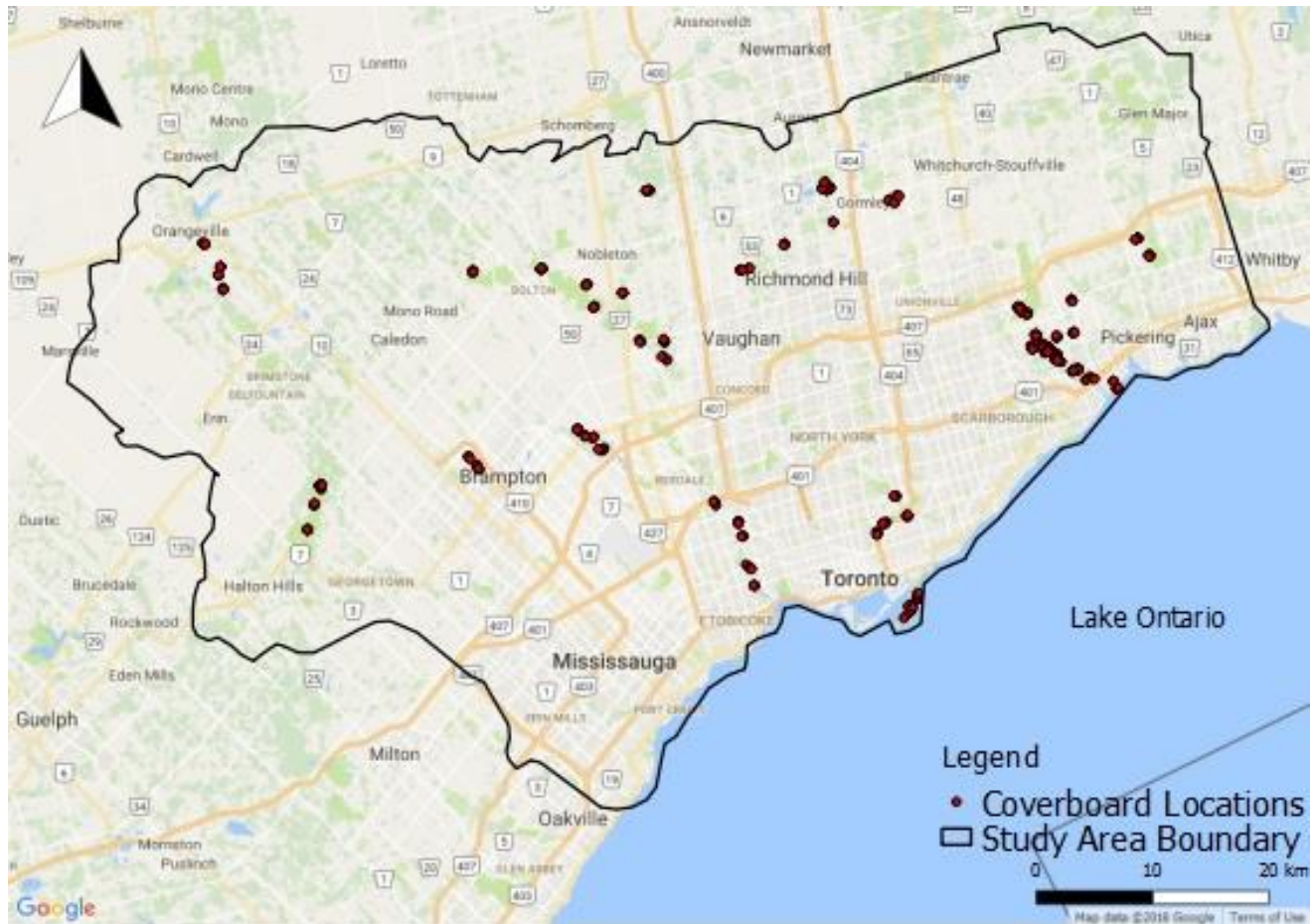
Figure 5. Map of the study area boundary is indicated by the black line. Snake survey locations (i.e., coverboards) are indicated by the red circles. Study area boundary was defined by combining the Toronto Region Conservation Authority and Credit Valley Conservation Authority boundaries. Major highways, cities, and natural areas (in green) can also be seen in the background layer.

4.2.2 Occurrence and Absence Locations

Snake occurrence records were generated from 2015-2017 using a large scale coverboard survey (Figure 5) as coverboards represent an effective low maintenance means of monitoring herpetofauna (Grant et al., 1991). All boards were made of untreated plywood (dimensions 120cm x 80cm x 2cm) and were placed between 2011 and 2015 based on historic snake occurrence records, primarily incidental observations, obtained through the Natural Heritage Information Centre (herein NHIC) (Figure 11, Figure 12). During checks, I visited all boards at a given site recording environmental data (cloud cover, temperature, humidity), temperature under each board, snake species present, morphometric measurements, and collected blood or tissue samples from all snakes.

It is unlikely that contemporary snake populations have become established in areas with no historic records, as snake dispersal is constrained by roads, development, and agricultural fields (Lambeck, 1997; Mader, 1984). Due to the cryptic nature of milksnakes, I supplemented the coverboard survey occurrence records with: *(1)* TRCA incidental occurrences, *(2)* CVC incidental occurrences, and *(3)* road kill data collected by the Toronto Zoo (2011) in the Rouge Valley watershed. Garter snake records were supplemented by CVC incidental occurrences. I created 1:1 pseudo-absence locations by randomly generating locations within landcover cells that did not include occurrence points, and coded locations as 1 (occurrence) or 0 (pseudo-absence) (Barbet-Massin, Jiguet, Albert, & Thuiller, 2012; Wisz & Guisan, 2009). All milksnakes were identified by PIT tags or unique head markings, and repeat observations were not included as additional occurrence locations.

4.2.3 Covariate Development

I developed a large-scale land cover map using remote sensing data obtained from Agriculture & Agri-Foods Canada's (herein AAFC) 2014 crop inventory (AAFC, 2014). Multiple cover types were combined to create seven landcover layers prevalent within the study area Table 6). I derived six covariates from each landcover type including 3 density covariates and 3 decay distance covariates for a total of 42 landcover covariates (Carpenter, Aldridge, & Boyce, 2010; Nielsen, Cranston, & Stenhouse, 2009).

Table 6. Development of landcover layers used in the development of models and resource selection functions, including landcover types used in building each layer (AAFC, 2014). Denotation by ǂ indicates a human-modified landcover type.

Landcover Type	Inputs from AAFC Data	Description	Justification
Forest 30m x 30m	Broadleaf forest Mixed wood forest Coniferous forest Undifferentiated Forest	All predominantly trees landscapes.	Forest edges important for thermoregulation (Row & Blouin-Demers, 2006c).
Successional 30m x 30m	Shrubland	Woody vegetation, +/-2m in height.	Influential in home range-scale habitat selection (Chapter 2).
Wetland 30m x 30m	Wetland	Semi-permanent and permanent wetland vegetation, omitting open water.	Natural area network contains floodplains and wetland areas unsuitable for development
Grassland 30m x 30m	Grassland	Native grasses and herbaceous vegetation.	Commonly used for basking by snakes (Ralph Gibson & Bruce Falls, 1979).
Field ǂ 30m x 30m	Fallow field Pasture	Non-permanent grasslands subject to seasonal and annual changes, typically non-native species. Common in marginal agricultural lands.	Historic association with milksnake occurrence (COSEWIC, 2014)
Agriculture ǂ 30m x 30m	Cereal crops Legumes Vegetables Fruits	Several combined crops, representing all agricultural land use.	Negative association with snake occurrence (COSEWIC, 2014)
Urban ǂ 30m x 30m	Urban	All roads, railways, paved surfaces, urban residential, commercial, industrial, other buildings.	Negative association with snake occurrence (Chapter 2)

Density covariates were generated using 3 moving window$_{MW}$ sizes (250m$_{MW250}$, 500m$_{MW500}$, 1000m$_{MW1000}$) for each landcover type. Multiple scales were chosen to represent the highly

variable size and layout of natural areas in the study area, and scale dependent habitat selection processes in snakes (Chapter 2, Row & Blouin-Demers, 2006). Decay distance$_{DD}$ variables were created using an exponential decay function $e^{-a/d}$ where a was set at 250m$_{DD250}$, 500m$_{DD500}$, and 1000m$_{DD1000}$, d was the distance from a given cell to the given landcover type. Decay distances was chosen rather than linear distance due to species inherently non-linear responses to habitat, and due to known impacts of anthropogenic landcover on snake behaviour and populations (Corey & Doody, 2010; Ettling et al., 2016).

4.2.4   Model Development and Selection

I next determined which of the 6 covariates within each landcover type were the best predictors of occurrence for each species. Each covariate was assessed in a univariate generalized linear model (GLM) with a binomial link function used for presence-absence data. GLMs were chosen as they are ideal for use with presence/pseudo-absence data (Chefaoui & Lobo, 2008; Tsoar, Allouche, Steinitz, Rotem, & Kadmon, 2007). Each univariate model also included an intercept-only model for comparison. When the intercept-only model outperformed the univariate model, the variable was dropped from further consideration. Univariate models were ranked based on their ΔAIC values, and the model producing the lowest value was considered the top covariate for the given landcover type and species. This process produced a list of 7 unique landcover covariates representing the seven landcover types for each species.

I examined correlation between the 7 landcover covariates to ensure no pairs produced an unacceptable level of correlation (Pearson's r ≥ |0.65|) to avoid issues of multicollinearity. Using the top covariate for each landscape layer, I developed global models for both species using GLMs with a binomial link function to predict the probability of occurrence. I considered all possible model combinations for each species, ranked models based on AIC values, and selected the top

model (producing the lowest ΔAIC). All models within ΔAIC <2 were considered as potentially contributing to differences between occurrence and absence locations (Arnold, 2010). I examined top model covariates and inferred relationships between human disturbance and likelihood of occurrence from all top models. The top model was predicted spatially as a resource selection function (RSF) with a continuous 0-1 scale representing predicted probability of occurrence.

4.2.5   Model Evaluation and Comparison

I evaluated the performance of each RSF using the Boyce validation index (i.e. k-fold cross validation) (Boyce, Vernier, Nielsen, & Schmiegelow, 2002). Spearman-rank correlation was calculated between bins, and model performance was assessed based on the average Spearman-rank correlation across all bins (Boyce et al., 2002). High correlation values between bins suggests a model that preforms well in predicting likelihood of occurrence (Boyce et al., 2002).

To directly compare species, I used the landcover covariates from the top model from each species to model the other species, and compared the coefficients. To identify areas with the best predicted habitat for both species, I created an map summing the two RSF's. I considered all values above the third quartile of the probability distribution (i.e. top 25% of all pixels) for each RSF to constitute good habitat (Fedy, Devries, Howerter, & Row, 2018). These values were transformed to 1, and all values below the third quartile were coded as 0. The remaining values for both species were summed to produce a surface showing areas with best predicted habitat for 2, 1, or neither species.

4.3 Results

I placed 385 boards at 53 sites during the 2015 season and combined with the 88 boards placed at 2 sites by the Toronto Zoo in 2011, the coverboard survey included 473 boards at 54 sites. This generated 78 milksnake records and 82 gartersnake records through the coverboard survey, and supplemented these with an additional 114 milksnake records and 175 gartersnake records (Table 7).

Table 7. Summary of occurrence used in modelling and to develop resource selection functions.

Species	Coverboards	Roadkill Surveys	CVC	TRCA	Total
Milksnake	78	18	55	41	192
Gartersnake	82	0	58	117	257

4.3.1 Model Selection

None of the covariates were unacceptably correlated ($r < 0.6$). Univariate model comparisons consistently resulted in milksnakes responding (both positively and negatively) to habitat types at larger scales. Differing scale of responses to habitat types is most apparent in agriculture, forest, wetland, and grassland where milksnake univariate models preformed best at 1000m while gartersnakes did so at 250m.

All possible model combinations were compared ($n = 128$) for each species. Seven milksnake models and 3 gartersnake models were within ΔAIC <2 and were considered the top models. Of the top milksnake models, all contained covariates representing agriculture $_{MW1000}$, forest $_{MW1000}$, and wetland $_{MW1000}$ (Table 8) The top model consisted of only these 3 covariates, while 5 of 6 other top models were a combination of this model plus one additional covariates (Table 8) Of the top 3 gartersnake models, all contained agriculture $_{MW250}$, forest $_{DD250}$, wetland $_{DD1000}$, field $_{MW500}$ and urban $_{MW250}$, while the top model also contained grassland $_{DD1000}$ (Table 8). Coefficient estimates were consistently negative or positive across the top models.

Table 8.Milksnake and gartersnake model tables including all candidate producing ΔAIC values <2, and potentially contributing to occurrence locations.

Milksnake Model Formulas	ΔAIC
Occurrence~AgricultureMW1000+ForestMW1000+WetlandMW1000	*0*
Occurrence~AgricultureMW1000+ForestMW1000+WetlandMW1000+SuccessionalDD1000	*0.12*
Occurrence~AgricultureMW1000+ForestMW1000+WetlandMW1000+UrbanMW250	*0.64*
Occurrence~AgricultureMW1000+ForestMW1000+WetlandMW1000+FieldDD250	*1.49*
Occurrence~AgricultureMW1000+ForestMW1000+WetlandMW1000+SuccessionalDD1000+Field DD250	*1.57*
Occurrence~AgricultureMW1000+ForestMW1000+WetlandMW1000+SuccessionalDD1000+Urban MW250	*1.89*
Occurrence~AgricultureMW1000+ForestMW1000+WetlandMW1000+GrasslandDD1000	*1.99*
Gartersnake Model Formulas	**ΔAIC**
Occurrence~AgricultureMW250+ForestDD250+FieldMW1000+UrbanMW250+WetlandDD1000Gr asslandMW500	*0*
Occurrence~AgricultureMW250+Forest $_{DD250+FieldMW500+UrbanMW250+Wetland\ DD1000}$	*1.30*
Occurrence~AgricultureMW250+ForestDD250+FieldMW500+UrbanMW250+WetlandDD1000+G rasslandMW500+SuccessionalDD1000	*1.78*

The top models for both species contained positive coefficient estimates for forest and wetland and negative estimates for agriculture (Figure 6, Figure 7). None of the coefficients in the top models had 85% confidence interval that overlapped zero (Figure 6, Figure 7). Milksnakes showed less consistent negative association with human modified landcover types urban (2 models) and agriculture (all competitive models) across all competitive models. However, urban did produce negative coefficient estimates in these two competitive milksnake models. Effects plot demonstrate similar negative responses to urban and agriculture, while responses to field vary between species (Figure 8).

4.3.2   Resource Selection Functions

Both RSF's had high Spearman correlation between bins for occurrence locations and therefore strong predictive capacity (EMS mean correlation = 0.98, EGS mean correlation = 0.92).

4.3.3   Species Comparisons

Comparing the top milksnake model between species, it is clear that milksnakes select for or select against fewer landcover types at larger spatial scales. Applying gartersnake date to the 3

landcover covariates from the milksnake, it is clear that selection and avoidance at these scales is stronger in milksnakes. Best predicted habitat for both species is primarily available through the Greenbelt areas north of the study area and the Rouge Valley to east of the study area. Relatively continuous habitat is available through these areas, while all locations through the core of the GTA have isolated patches of best predicted habitat (Figure 9). Comparing this map to the RSFs, it is apparent that best predicted habitat for both species is constrained by the availability of highly suitable milksnake habitat (Figure 10).
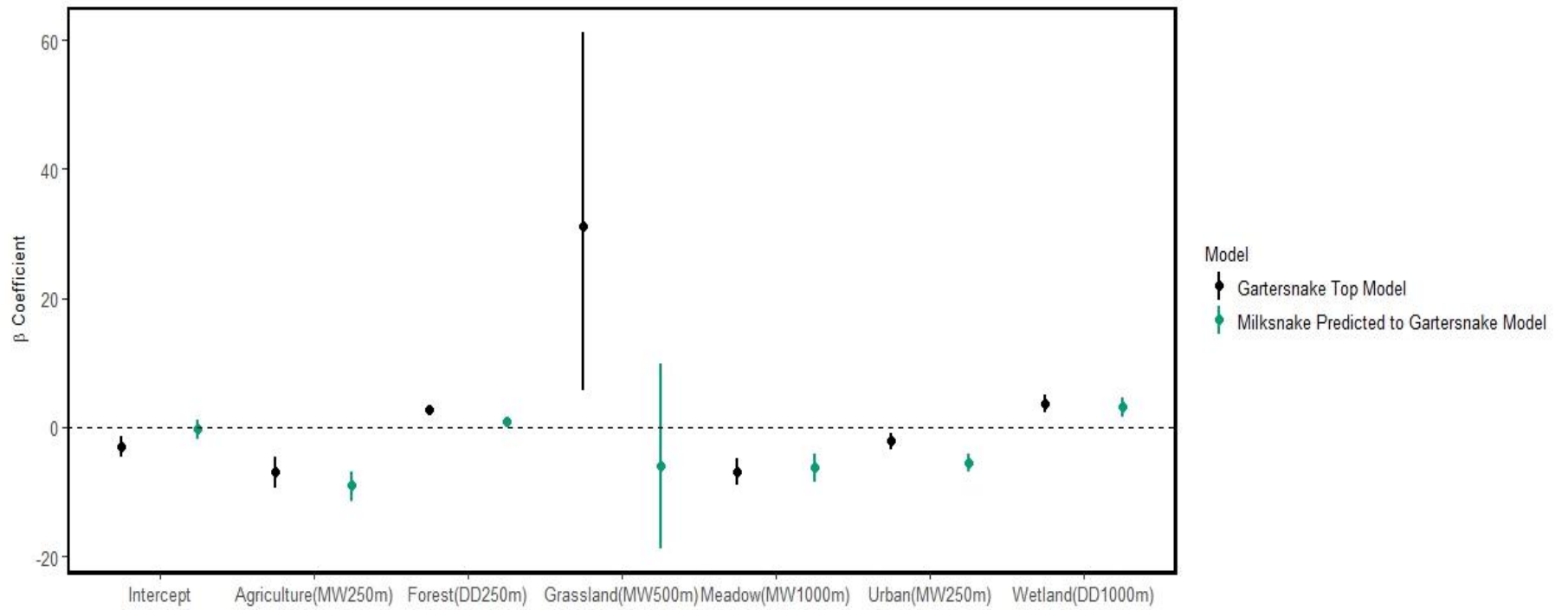
Figure 6. Coefficient estimates from gartersnake top model. Coefficients for milksnakes, produced using the landcover covariates from the gartersnake top model, are also displayed.

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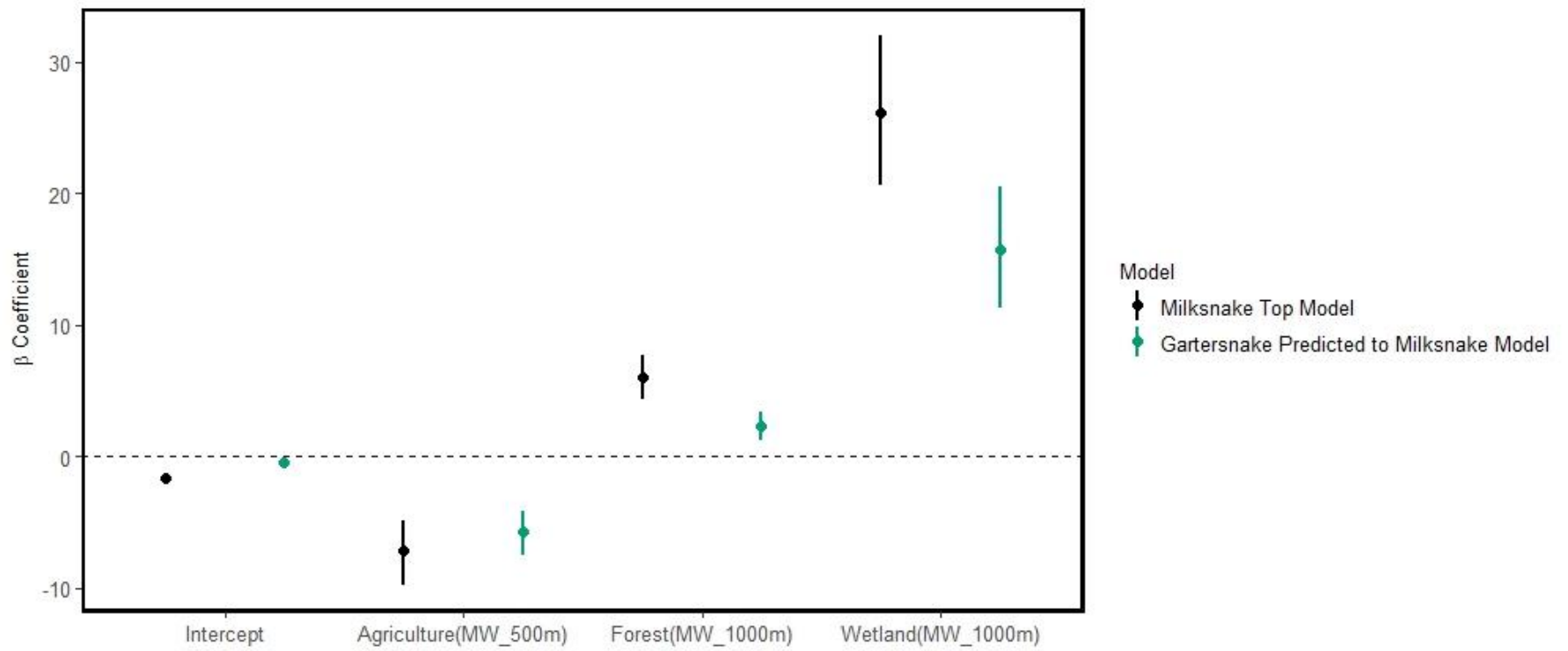
Figure 7. Coefficient estimates from milksnake top model. Coefficients for gartersnakes, produced using the landcover covariates from the milksnake top model, are also displayed.

Eastern Milksnake

Eastern Gartersnake
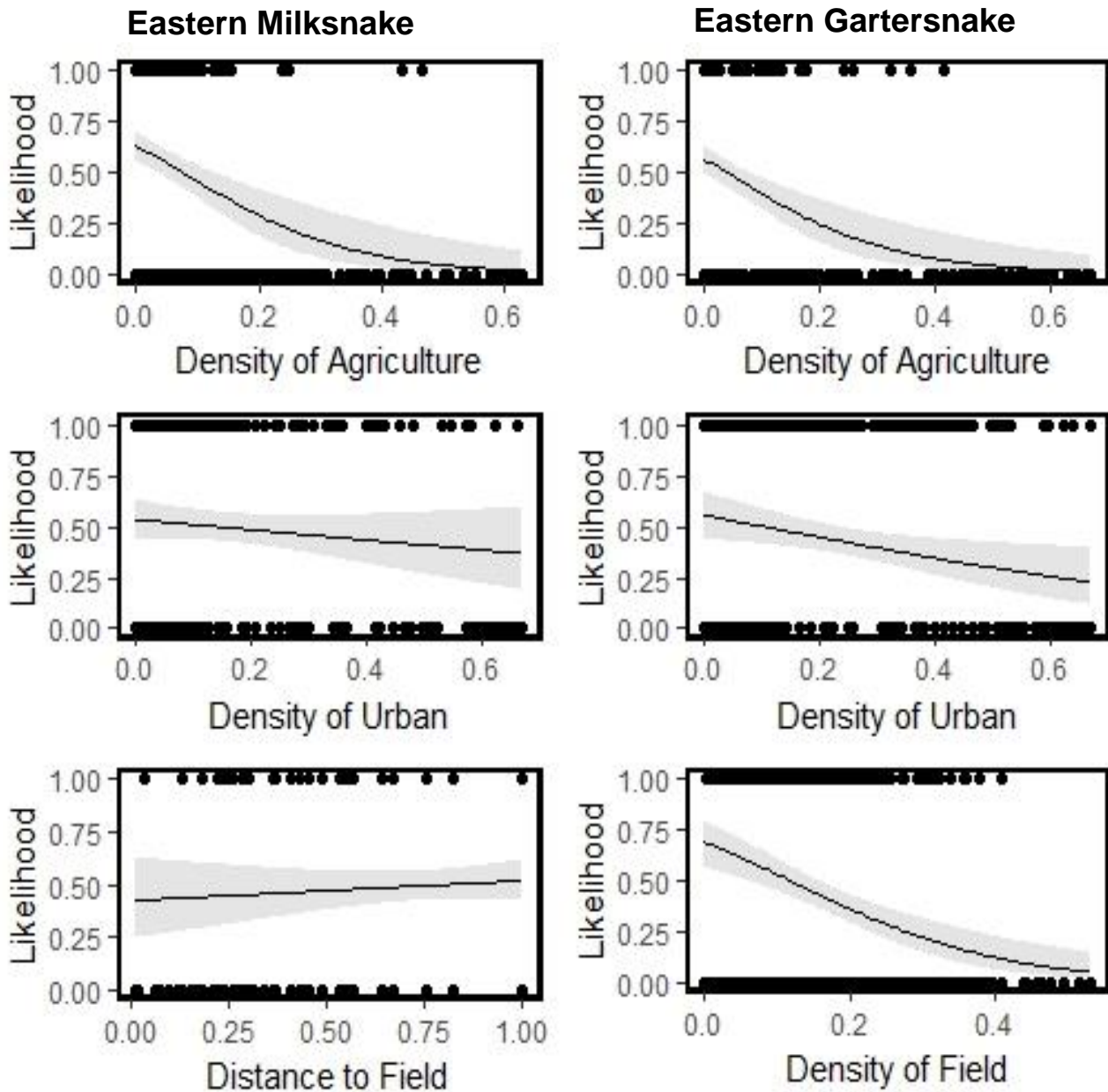
Figure 8. Responses to human modified landcover types by milksnakes (left) and gartersnakes (right) and the data used to generate response curves and associated standard error (shown in grey).
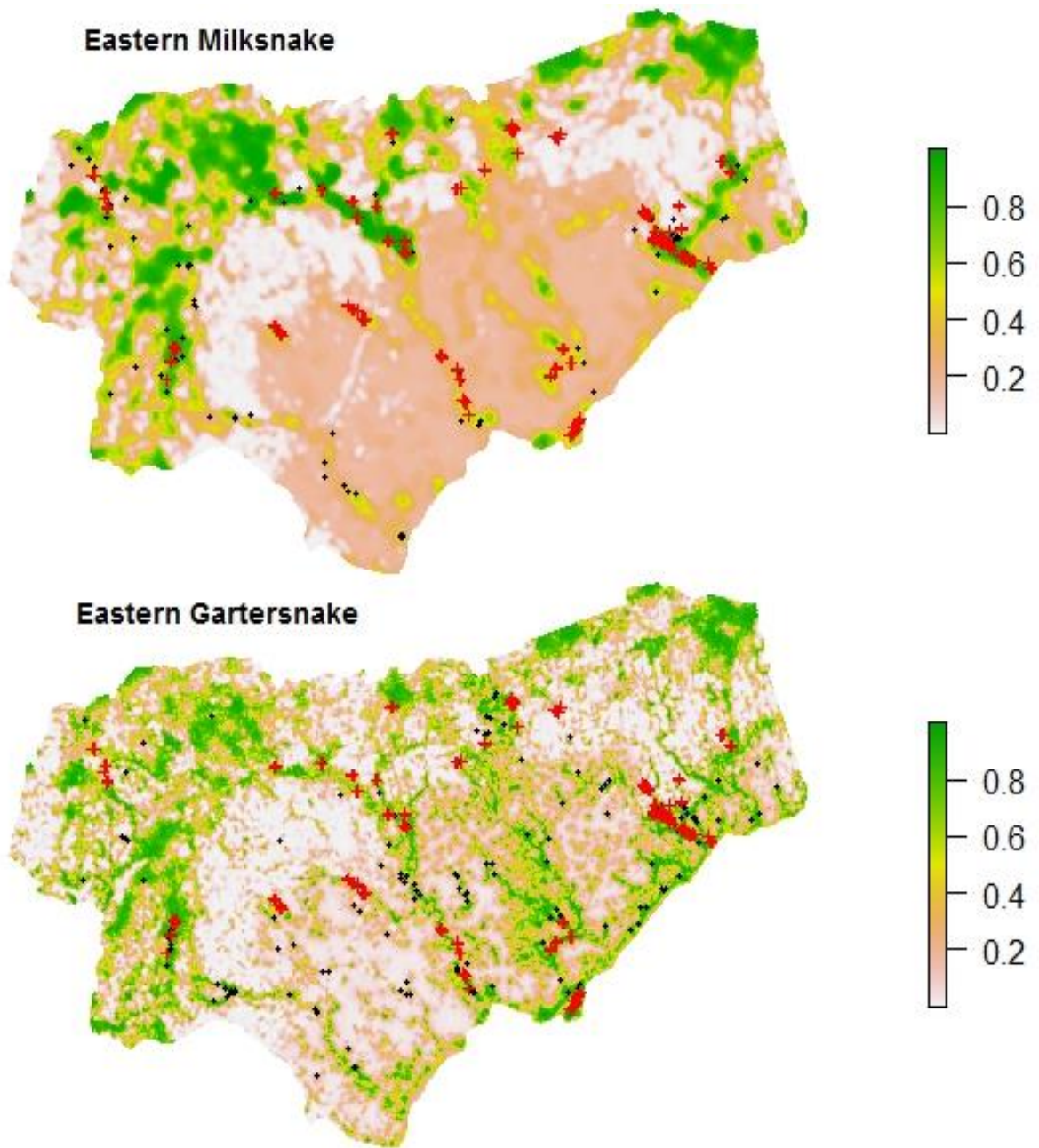
Figure 9. Resource selection functions for eastern milksnake and eastern gartersnake including all occurrence locations (black) used in model development and coverboard locations (red) used to gather occurrence records. Scale bars represent increasing relative probability of occurrence.
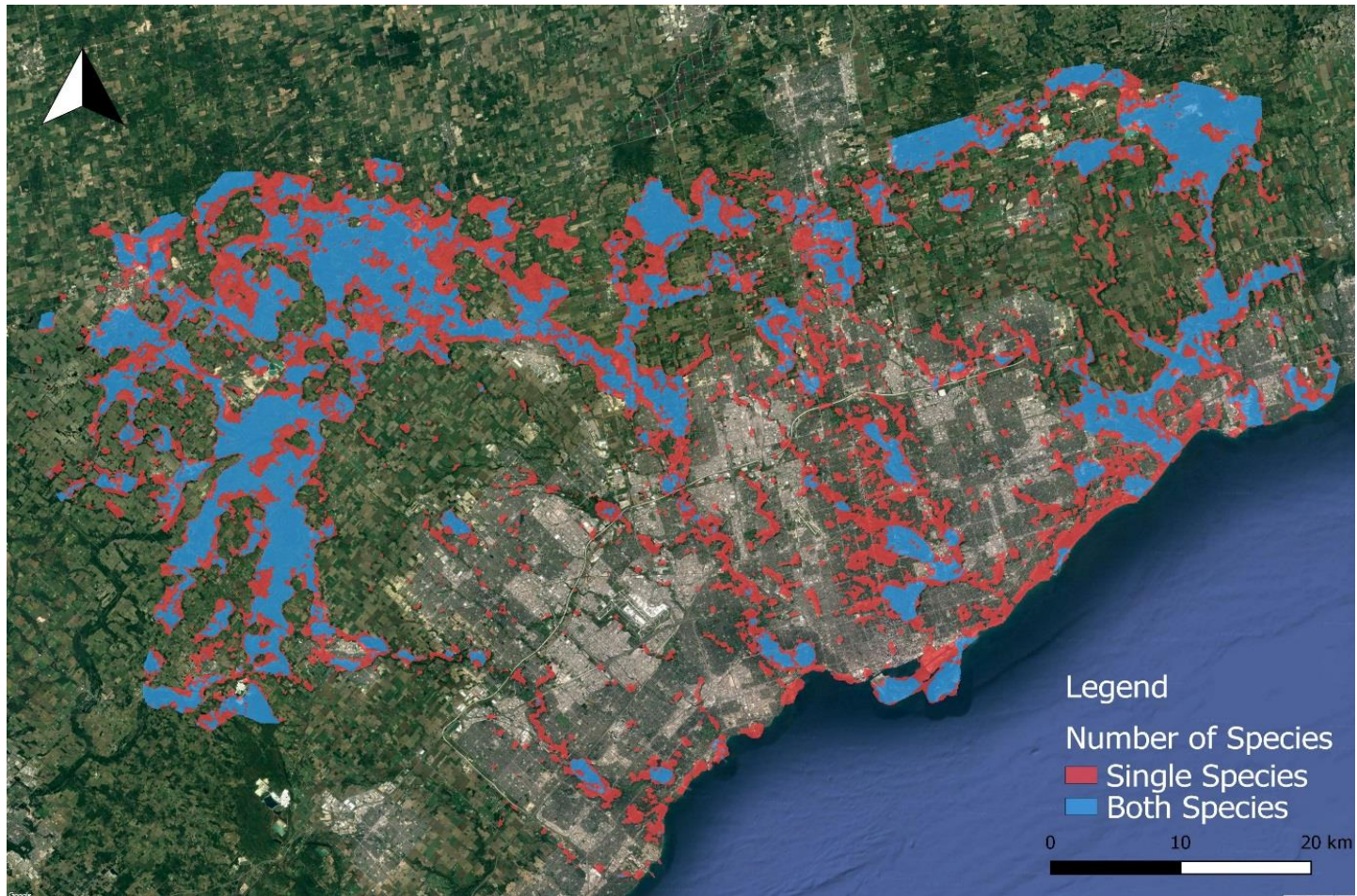
Figure 10. Areas with high likelihood of occurrence for gartersnake and milksnake (blue), or one of these species (red) within the study area. Areas with low likelihood of occurrence for both species are not highlighted.

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4.4   Discussion

The generalist and specialist species focused on in this research demonstrated differential patterns of habitat use consistent with their life history strategies across a highly fragmented region. The top model set for the specialist species, milksnakes, contained a greater number of models having generally fewer variables than the generalist species, gartersnakes. The suite of top milksnake models had consistently positive coefficient estimates for forest and wetland cover which were also present, though at smaller scales, in the top gartersnake models which also all demonstrated negative associations with fallow fields and pastures (field). Both species avoided human-modified landscapes represented by agriculture cover, and the top gartersnake models also indicated avoidance of urban areas. There is also a notable difference in the scale at which each species responds to landcover types, as milksnakes consistency responded to habitat types at larger scales. This is evident in the maps of predicted likelihood of occurrence as smaller patches of natural area surrounded by human modified landscapes are not suitable for milksnakes, leading to best predicted multi-species habitat being constrained by milksnake occurrence.

The competitive model sets indicate that the milksnakes have more specific habitat requirements as they contain fewer variables. This is consistent with my prediction, and other literature demonstrating that habitat selection models for specialist snake species result in a stronger response to fewer natural landcover types than generalist species in the same region (Segura, Feriche, Pleguezuelos, & Santos, 2007). Previous research has demonstrated that milksnakes use forest edge habitats for thermoregulation, and this is supported in the landscape-scale study in the positive association with forest cover (Row & Blouin-Demers, 2006c). Snake species in forested landscapes also make use of small open habitat patches (Kjoss & Litvaitis, 2001) created by micro disturbances as small as single treefall events (Canham et al., 1990), which

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would be difficult to detect at the spatial resolution of the data. Resolution may also explain why successional habitat is important at the micro-habitat and home range scales for milksnakes (Chapter 2), but does not influence likelihood of occurrence at the landscape scale.

Surprisingly, the avoidance of urban areas was more prevalent in the top models for gartersnakes than milksnakes, contrary to my prediction that milksnakes would demonstrate greater avoidance than gartersnakes. The negative association with agriculture by gartersnakes and scale of the response (250m) suggests that gartersnakes use habitats directly bordering agriculture. Gartersnakes are known as dietary generalists (Kephart & Arnold, 1982), and generalist snake species can modify behaviours to use crop monocultures and intensive agricultural areas when prey is abundant in these areas (Ettling et al., 2016; Wisler, Hofer, & Arlettaz, 2008). While the results show avoidance of agriculture, the scale of the response and species biology suggest they may occasionally use these areas. The slight positive response in milksnakes to increased distances from field$_{DD250}$, compared to gartersnakes strong negative response to density of field$_{MW1000}$ can be attributed to species life history. Milksnakes are historically associated with low intensity agriculture and make frequent use of human structures (i.e. barns, buildings) in these landscapes (COSEWIC, 2014; Lentini et al., 2015; Row & Blouin-Demers, 2006c). Agricultural fields taken out of production and low intensity agriculture have been noted to benefit other specialist snake species (Kjoss & Litvaitis, 2001; R Shine & Fitzgerald, 2006). However, this habitat type occurs infrequently in the study area as low intensity agricultural areas are in decline, in favour of larger scale farming (Gallant et al., 2007) The negative association with urban areas is also consistent between species. However, the data do not include between type (i.e. detached homes, high rises) or age of urban development, which is influences natural area patch size and herpetofauna occupancy (Vignoli et al., 2009).

Milksnakes consistently responded to landcover types at larger scales than gartersnakes as they are more sensitive to disturbance and require larger tracts of suitable habitat. The conservation of coastal and riparian wetlands is a priority at the landscape scale within in the study area (Croft-White, Cvetkovic, Rokitnicki-Wojcik, Midwood, & Grabas, 2017). The conservation of these areas and relative lack of human disturbance likely influences the strong positive associations for both species to wetland habitat types at the same scale ($MW1000, DD1000$). Milksnakes are also selecting forest habitat ($MW1000$) and avoiding agriculture ($MW1000$) and urban ($MW1000$) habitat at much larger scales than gartersnakes ($DD250, MW250, MW250$). This is evident in the spatially precited RSF`s, as suitable gartersnake habitat can often follow small corridors of natural habitat adjacent to urban areas, whereas these habitats are normally considered to be unsuitable for milksnakes. Minimum area requirements for specialist species are often not met in areas of intensive development (Vignoli et al., 2009) and these impacts are compounded because milksnake home ranges are much larger than gartersnakes (Kjoss & Litvaitis, 2001, Chapter 2).

Suitable habitat patches large enough for milksnakes likely do not exist in direct proximity to urban and agricultural areas in the study region. The best predicted multi-species habitat is then limited by milksnakes, meaning prioritization of milksnake habitat would also adequately conserve gartersnake habitat. These findings offer some support for the use of focal species in conservation prioritisation where species have known range overlap (Bifolchi & Lodé, 2005; Roberge & Angelstam, 2004). While this approach would neglect small patches of suitable gartersnake habitat, these patches are comprised of parkland and riparian areas that are not under further development pressure. The best predicted multi species habitats found in the study area occur in larger natural areas and along an ex-urban gradient. Large, well-connected, natural areas are consistently shown to benefit specialist species in fragmented landscapes (Lees & Peres, 2009;

Tischendorf, Bender, & Fahrig, 2003) and this appears to be the case for milksnakes in this study. However, these ex-urban areas are facing increasing development pressure (Gallant et al., 2007; Recio et al., 2015). Without effort to protect ex-urban areas including low-intensity agriculture and large tracts of forest and wetland habitats, intensive agriculture and development will likely have long term negative effects on milksnake and gartersnake populations.

Milksnakes, a specialist species, are selecting fewer habitat types as being suitable at larger scales than gartersnakes, a generalist species. As predicted, high quality multi-species habitat is driven by the distribution of milksnakes which typically contains habitats also suitable to gartersnakes. In order to effectively conserve both species, conservation of the remaining larger natural areas along an ex-urban gradient should be prioritized. In the context of the GTA, this should focus on preserving existing habitat along the north end of the Credit Valley and Toronto Region Conservation Authority management areas, and northeast end of the study area which is currently facing development pressures.

5 Conclusions

This study quantifies milksnake habitat selection and behavioural adaptation in response to human development. My results indicate changes in movement rates and habitat selection patterns in disturbed areas, potentially due to constraints by roads and an unwillingness to make crossings. Though the study area is highly fragmented, these findings come from relatively large patches. In order to fully understand the impact of roads, future research should estimate population size and genetic distribution to understand source-sink dynamics of individual habitat patches. Milksnakes avoid urban areas, interior forests, and agricultural fields at the home range scale, while selecting for successional habitat. Microhabitat selection favors heterogeneous locations near forest edges (higher surrounding structure, but low at-site vegetation) with low canopy cover, and abundant cover, likely owing to a trade-off between thermoregulatory benefit and predator avoidance. Selection for open habitats and abundant cover is consistent with what is known to occur in natural landscapes

At the landscape scale, milksnakes (a specialist species) and gartersnakes (a generalist species) were found to have differential patterns of habitat selection both in terms of habitat type and the scale at which selection is occurring. Both species appear to be selecting for forest and wetland habitat, and avoiding urban and agricultural areas. This response is occurring at different scales, with milksnakes consistently responding at larger scales which indicates increased avoidance of human modified landscapes and a preference for large natural areas. Gartersnakes occur throughout highly fragmented landscapes, as they are able to use small habitat patches unsuitable for milksnakes. High quality multi species habitat is then limited by the distribution of milksnakes, and occurs primarily in the northern end of the TRCA and CVC management areas, and the northeast end of the study area.

Overall, I recommend the restoration of marginal agricultural areas surrounding existing natural corridors to meadow and successional habitat to allow for movement between patches. Selection for forest and wetland at the landscape scale means that priority should also be put on expanding or maintaining large natural areas, which would effectively conserve habitat for both milksnakes and gartersnakes. This would also create an abundance of edge habitat, and would allow current forests to age and create micro-disturbances which lead to suitable microhabitats. It should also be notes that areas selected as parts of natural corridors should contain milksnake populations, as the number of roads in the study area limits dispersal to suitable habitat patches. If populations do not exist, efforts should be made, potentially through the use of underpasses, to connect suitable habitats. This requires future research to estimate population sizes in different habitat patches, and assess genetic connectivity of populations, in order to understand patch source/sink dynamics. The presence of RNUP in the study area creates a potential refuge for milksnake populations. However, natural corridors containing a diversity of microhabitats and other large natural areas should be established to ensure long term persistence of milksnakes in the Greater Toronto Area.

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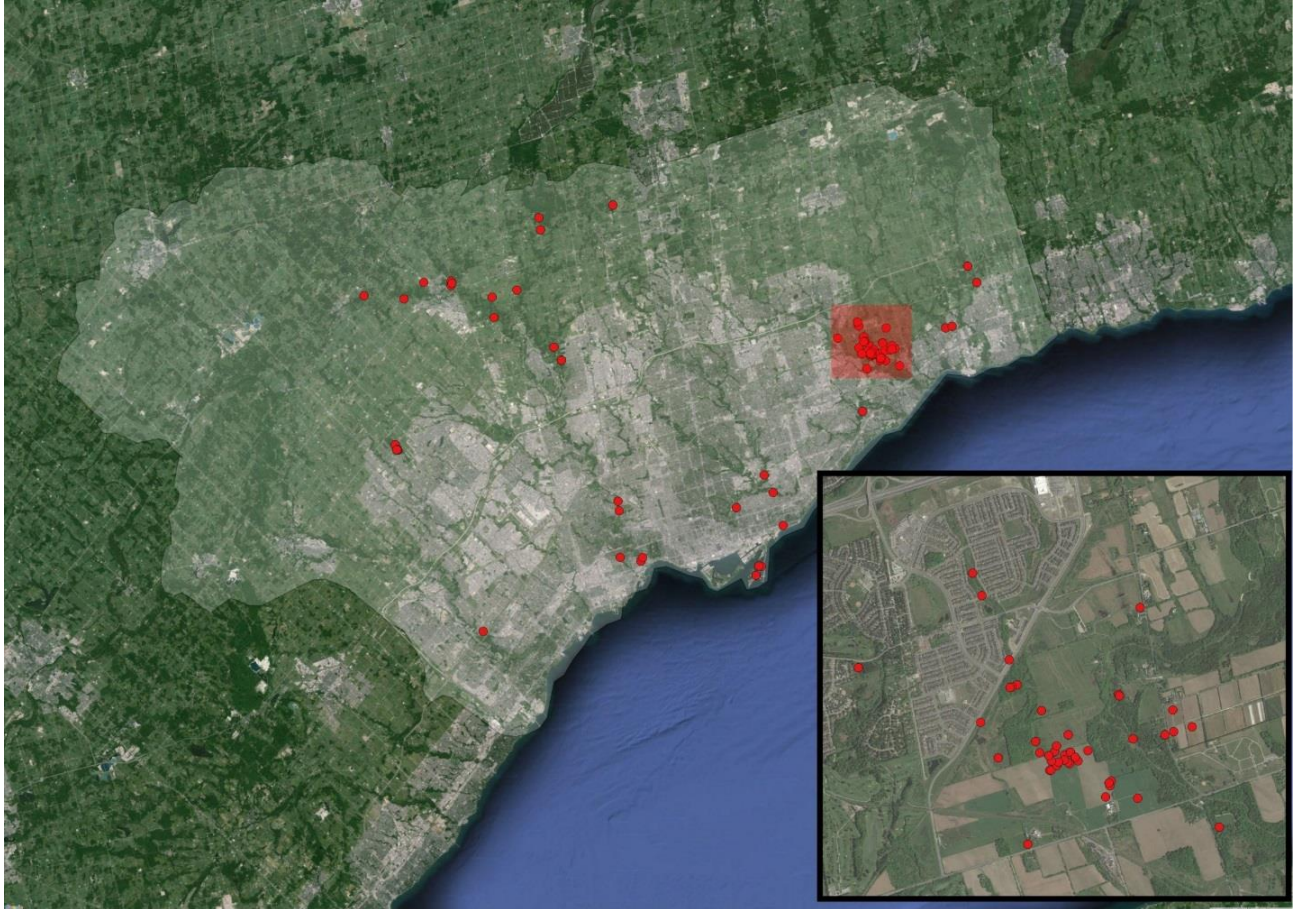# 7   Appendix 1: Supplementary Material

Figure 11. Map showing contemporary (post-2000) occurrence of milksnakes in the Credit Valley and Toronto Region Conservation Authority management areas. It is evident that current distribution is limited to larger natural areas, with some occurrence records present in small, more urban natural areas.
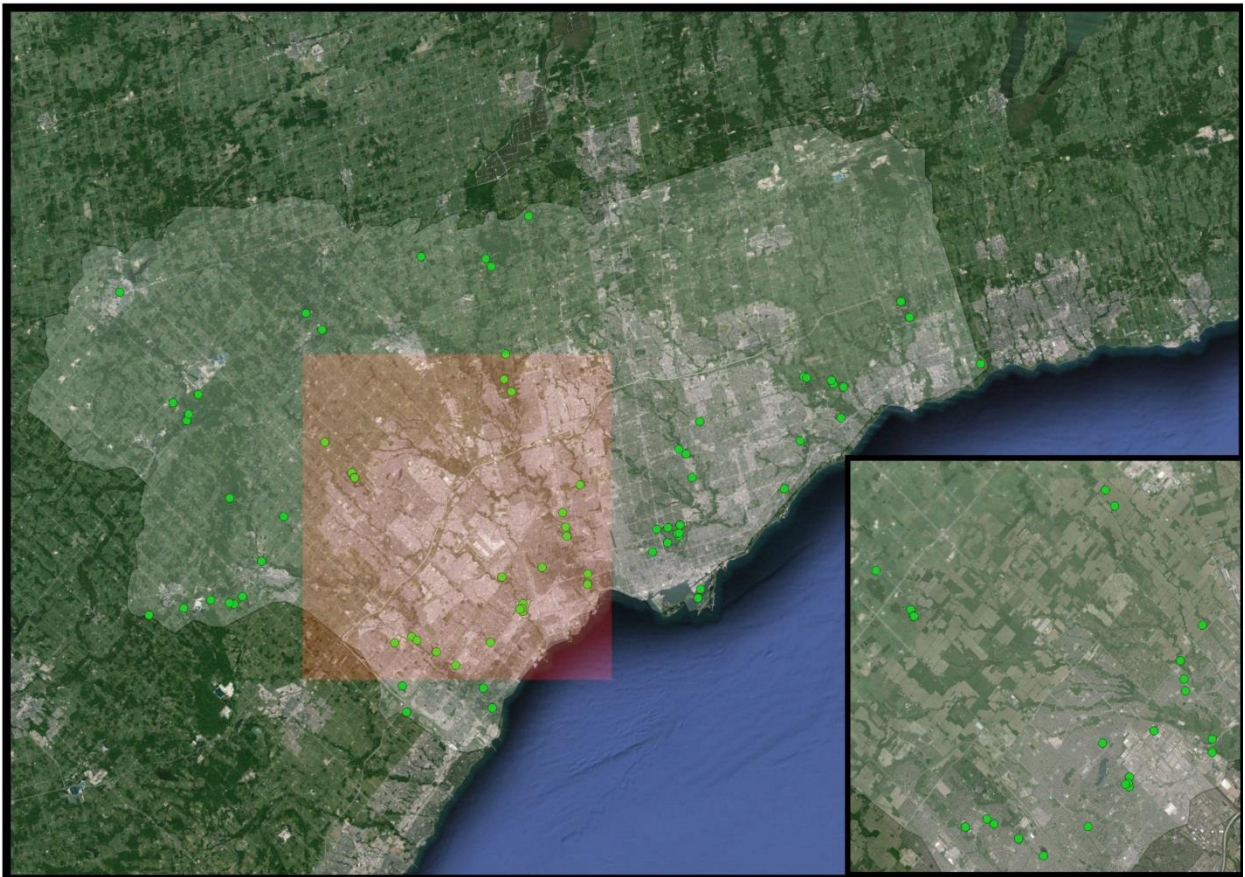
Figure 12. Map showing historic occurrence records (pre-2000) of milksnakes in the Credit Valley and Toronto Region Conservation Authority management areas. The background layer used is contemporary, and highlights the amount of urban development through areas of historic occurrence.
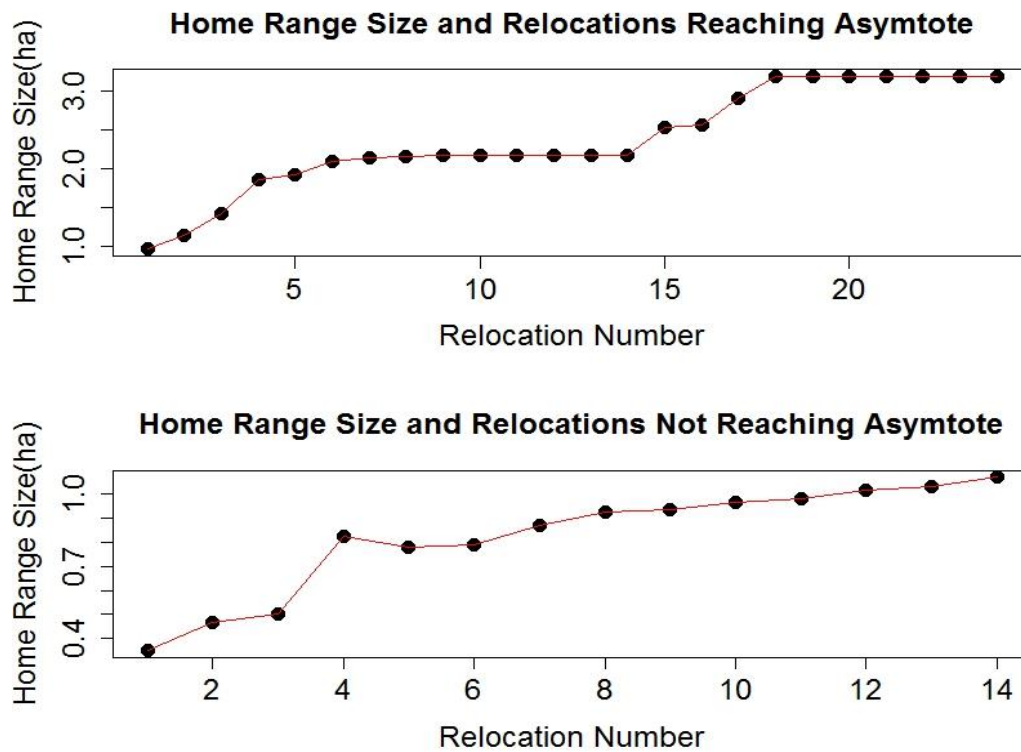
Figure 13. Sample plots of individuals whose home range did and did not reach an asymptote. Plots were created by plotting home range size against number of relocations. Those that reached an asymptote were thought to have accessed their entire home range during the study period, and were included in home range analysis.
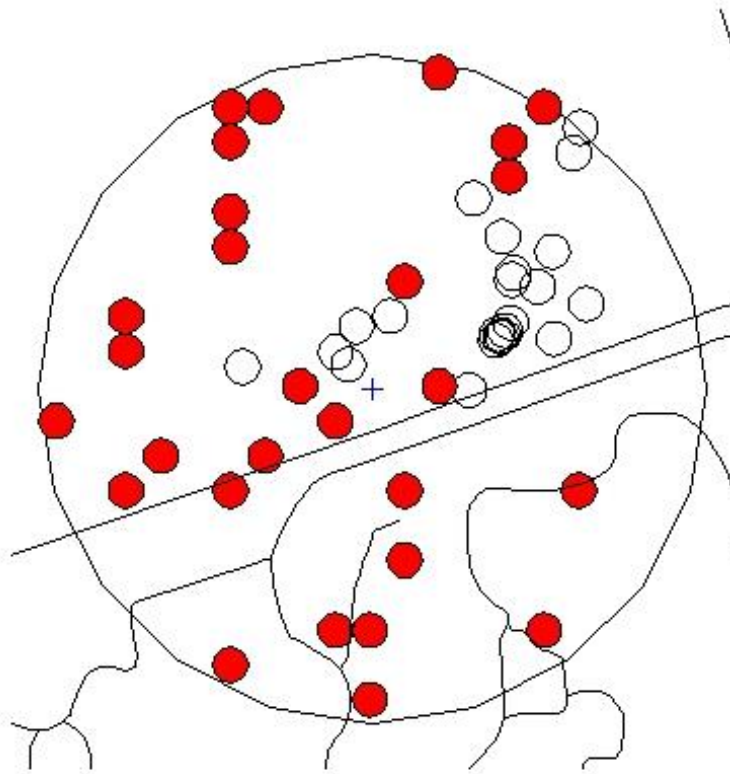
Figure 14. Example of used (white) and available (red) plots used in determine home range scale habitat selection, including roads. The central point represents this individual's hibernation site, and the large circle is a radial plot of the maximum distance travelled from the hibernation site. Random plots were generated in an area theoretically accessible to the individual based on maximum dispersal distance from the hibernaculum.
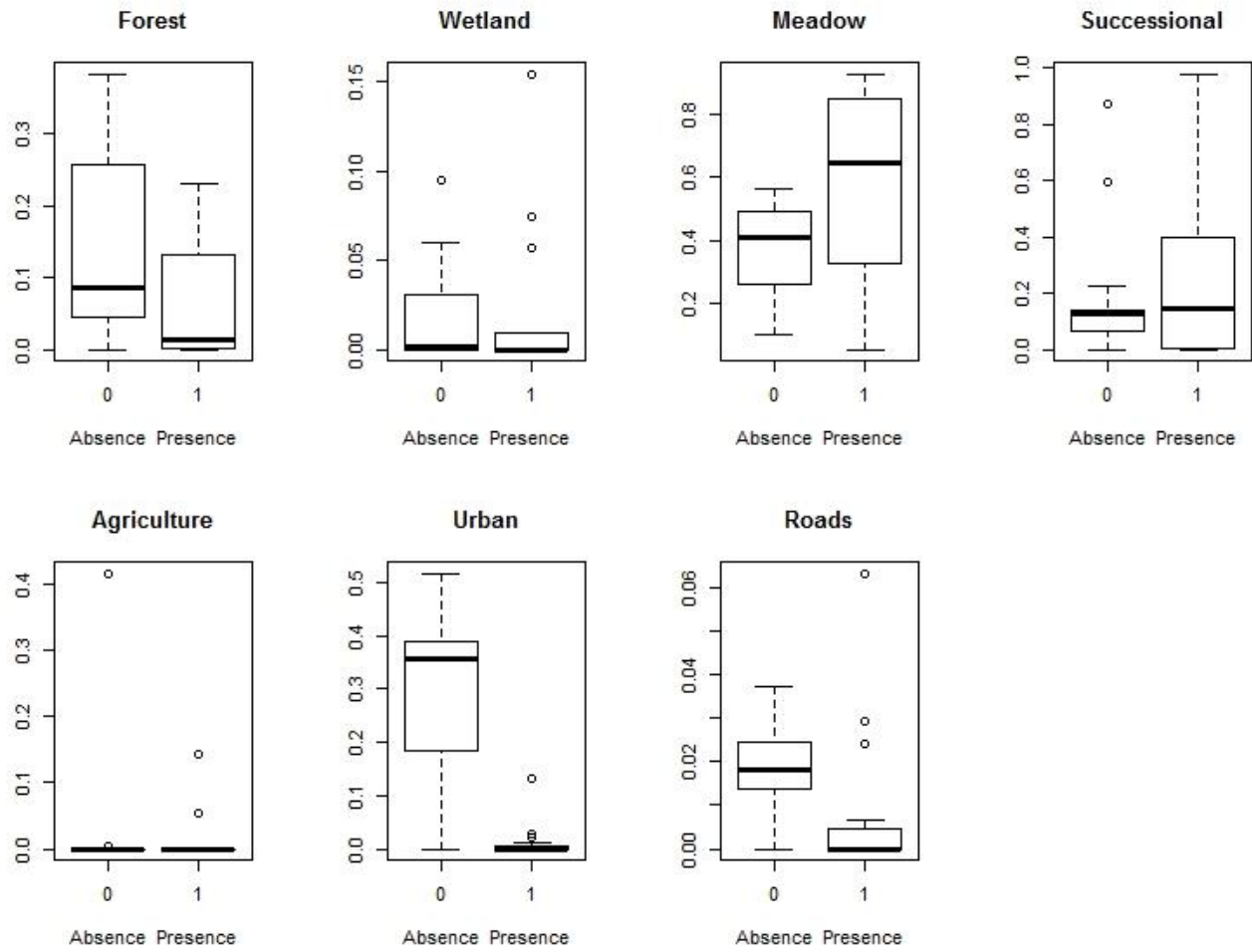
Figure 15. Mean covariates for each individual used in modelling home range habitat selection. Presence and absence locations are shown separately here for all seven landcover covariates used in modelling. While some outliers are present, the scale reveals relatively they are generally very minor, and may not be influential in modelling.

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