SPATIAL ECOLOGY AND VARIABLES INFLUENCING HABITAT USE AND FITNESS PROXIES OF EASTERN HOG-NOSED SNAKES (*HETERODON PLATIRHINOS*) WITHIN AN ANTHROPOGENIC LANDSCAPE

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ACCESSIBILITY CLAUSE AND PERMISSION TO USE

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Thesis Abstract

Changes in environmental conditions and threats from human activities present unique challenges to persistence and management of wildlife populations at range peripheries. For successful recovery and conservation of reptile species at risk (SAR), basic knowledge of their life histories and ecologies must be understood. Such basic information was lacking for a recently reported population of eastern hog-nosed snakes (*Heterodon platirhinos*) in southwestern Ontario. To successfully meet government-mandated recovery actions for the population of Threatened snakes, I investigated whether hog-nosed snakes' space use, habitat preferences, and proxies of fitness were impacted by widespread anthropogenic activity in Huron County, Ontario. I estimated movement and home range size (mean ± SD) from locations of hog-nosed snakes (n = 10) outfitted with radio transmitters from the 2018 to 2020 active seasons, and then calculated using kernel density estimates (KDE) and minimum convex polygons (MCP). I evaluated habitat selection at three scales (i.e., exact, local, and landscape) using resource selection function models and ranked models using Akaike's Information Criterion corrected for small sample sizes. Proxies of fitness I assessed included quantification of thermal habitat from hourly ground temperatures and snake body condition estimated from residuals of body mass on snout-vent length regressions. I found that when compared to conspecific populations throughout their range, Huron County snakes moved greater distances (49 ± 13 m per day, 127 ± 41 m per move) within larger-sized home ranges (64 ± 30 ha), as well as were heavier and in better body condition compared to conspecific populations near Point Pelee, Ontario. At the coarsest scale, I found that occurrence of snakes in Huron County was positively associated with forest, beach, and old field habitats, while at finer scales, habitat characteristics with structural complexity, cover, and thermal suitability influenced snake occurrence. While proxies of snake fitness did

not appear imminently impacted by human activity in Huron County, widespread disturbance did influence how hog-nosed snakes used the landscape: snakes moved greater distances (than those in conspecific populations) to use pockets of natural habitats that were thermally suitable and structurally complex. To ensure effective management of the population stewardship efforts should focus on protection and enhancement of snake habitat and have such actions follow recommendations from this study. My study exemplifies the complex nature of SAR management in Ontario and how understanding space use, habitat selection, and fitness proxies are important to successfully conserving and recovering a snake species at risk.

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pave the way for you continue to live out your best snake lives! A final outpour of love goes to my friends and family who, even from thousands of kilometers away, supported me on my journey to becoming a ‘Master Snake Whisperer’.

Dedication

I wish to dedicate this thesis to my little sister, Maya, who I hope to inspire and make proud, even though progressing my academic career has come at the cost of being away as you blossom. As well as dedicating this to the late, furry loves of my life, Oliver and Lexy, I hope that from above you know that leaving was the most difficult sacrifice to pursuing this journey.

General Introduction

Reptile Threats

Habitat loss, degradation, and fragmentation are considered the biggest threats to reptile persistence (Alford and Richards 1999; Gibbons et al. 2000; Lesbarrères et al. 2014), largely because reptiles rely on their environment for food, refugia, and thermal habitat (Waldschmidt and Tracy 1983; Hertz et al. 1993; Grover 1996; Seburn and Seburn 2000; Blouin-Demers and Weatherhead 2002; Row and Blouin-Demers 2006a.; Lienart et al. 2014). Degradation of critical habitats reduces opportunities for foraging (Shine et al. 1998; Kjoss and Litvaitis 2001), thermoregulation (Pike et al. 2010; Kay et al. 2016) and oviposition (Bolton and Brooks 2010; Cook et al. 2018) and impacts the ability to move between areas of critical habitat (Lesbarrères et al. 2014; Rotem and Ziv 2016; Markle and Chow-Fraser 2018). As a result, demes within metapopulations (Gill 1978; Seburn and Seburn 2000) that depend on each other for recolonization after stochastic depletion events (Hecnar 1997; Seburn and Seburn 2000) can also be compromised by anthropogenic barriers. Impeding movement between, or access to, critical resources can negatively affect the demographic structure and stability of populations (Seburn and Seburn 2000; Smith and Green 2005; Wolf et al. 2013; Walkup et al. 2017).

Introduction of non-native species also threatens reptiles and their habitat, impacting resource availability and acquisition, competition, species abundance, and further threatening habitat quality. Invasive exotic plants in particular, readily outcompete indigenous plant species with various competitive (toxin release into surrounding soil; OMNR 2011), reproductive (seeds, rhizomes, stolon fragments; OMNR 2011), and transmission strategies (air, water, vehicles, horticultural trade; OMNR 2011; National Wildlife Federation 2019), subsequently altering the surrounding vegetation communities. Restructuring of vegetation communities can lead to changes in resource distribution and availability (Heisler et al. 2013), which for reptiles can equate to a reduction in availability and quality of foraging, nesting, and thermoregulatory habitat (Markle et al. 2018). For example, the spread of Eurasian *Phragmites* (*Phragmites australis australis*) has displaced important critical habitat for reptiles in Point Pelee National Park, Ontario (Markle et al. 2018). In 2015, over 90% of the *Phragmites* grass displaced marsh habitats in Point Pelee National Park, while another 10% of the *Phragmites* invasion overwhelmed open water and dune habitats (Markle et al. 2018). The loss of or inability to access otherwise critical resources due to the colonization by exotic vegetation thus likely contributes to the declining trend of some reptile species (Bolton and Brooks 2010; Kapfer et al. 2013; Markle et al. 2018).

Direct interactions between humans and reptiles also create obstacles to reptile conservation. Some species are regarded as unlikable and feared (Thorpe and Salkovsis 1997; Yorek 2009), which is especially true for snakes who are subjected to deliberate persecution, from commercialized killing events like 'rattlesnake round-ups' (Fitch 1998; Cummins 2019), to intentionally being hit with motor vehicles (Langley et al. 1989; Seburn and Seburn 2000; Ashley et al. 2007; Secco et al. 2014). Persecution can lead to large reductions or complete extirpation of populations (Seburn and Seburn 2000; Todd et al. 2010; Marshall et al. 2018). Collecting wild animals for the pet trade also can be detrimental, as individuals removed no longer contribute to population persistence. Not all reptile species are legal to own, and demand may be higher than legal collection limits allow (Seburn and Seburn 2000) thus incentivizing illegal collection. Overharvest can negatively impact reptile populations, particularly for long-lived reptiles like turtles and some snakes with 'slow' life histories (Meffe and Carroll 1997;

Todd et al. 2010), who take years to reach sexual maturity (Congdon et al. 1994; Lovich et al. 2018; Maron 2019) or for populations that are already small (Congdon et al. 1993).

Reptile Fitness and Habitat Selection

Maslow's *Hierarchy of Needs* (1943) describes how an organism is limited by external circumstances to carry out basic life requirements. Thus, organism success is dependent on the quality of external conditions, and this is particularly true for reptiles, which rely on their environment to regulate body temperatures. Unlike endotherms that generate internal body heat via metabolism regardless of external conditions, ectotherms rely on the environment to regulate body temperature by changing their behaviour (Dzialowski 2005; Huey et al. 2012). Reptiles depend on exchanging heat with their environment for daily (digestion, locomotion, prey acquisition) and seasonal activities (growth, hibernation, embryo development; Gans and Pough 1982; Gardiner et al. 2015) that impact overall fitness. In temperate zones, temperature is thought to be one of the most imperative drivers of habitat selection (Reinert 1993), as reptiles consistently select microhabitats based on their thermal quality (Blouin-Demers and Weatherhead 2001a; Row and Blouin-Demers 2006a; Shoemaker and Gibbs 2010; Lelièvre et al. 2011; Robson 2011; Gardiner et al. 2015). For example, edge and open canopy habitats offer thermoregulatory qualities such as wider temperature ranges or increased solar radiation (Row and Blouin-Demers 2006a).

Resource availability also plays a key role in habitat selection. As the success of carrying out basic life requirements depends on quality of external conditions (Maslow 1943), organisms are largely influenced by resource acquisition and availability. Under the hierarchical process that habitat selection is understood (Johnson 1980), availability of resources is influential within the third and fourth orders, as how organisms use and select habitats is motivated by resource availability across the landscape (Buskirk and Millspaugh 2006). A species' geographical range comprises the first order of the hierarchy (Johnson 1980), laying the foundation for the second order, an individual's home range (Johnson 1980). A home range is defined as the space an individual routinely uses to complete essential activities, like foraging, mating, seeking refuge, and nesting (Burt 1943; Aebischer et al. 1993; Krebs and Davies 1997; Lelièvre et al. 2010). For reptiles, in addition to the aforementioned activities, the home range of a single individual also may contain distinct areas for thermoregulation and overwintering (Waldschmidt and Tracy 1983; Seburn and Seburn 2000; Innes et al. 2008). General habitat types within home ranges comprise the third order of habitat selection (Johnson 1980), while specific resources within such habitat types fall under the fourth order (Johnson 1980). Since availability and distribution of resources are major influences for habitat selection, resource availability also influences aspects of space use such as home range size (Boggie and Mannan 2014; Moorter et al. 2016; Edkins 2017). When animals that inhabit resource-deficient areas seek out and explore new areas for available resources the search results in larger home range sizes (Okarma et al. 1998; Mattison et al. 2013), which for animals that reside in human-modified areas has been a frequently observed phenomenon (Durner and Gates 1993; Ettling et al. 2013 & 2016).

Availability of cover is a key resource that drives reptile habitat selection. Accessibility to cover can mean life or death for reptiles, particularly when avoiding abiotic threats. As ectotherms are profoundly influenced by their external conditions, reptiles must seek refuge during extreme temperatures and climatic conditions (Huey and Kingsolver 1993; Blouin-Demers and Nadeau 2005; Blouin-Demers and Weatherhead 2008; Aragon et al. 2010). Refuge availability is particularly important for reptiles in northern temperate climates that experience daily and seasonal temperature extremes and fluctuations (Gardiner et al. 2015; Johnson et al.

2022). For snakes in temperate zones, suitable cover can include logs, leaf litter, sandy soils that facilitate burrowing, shrubs, and mammal burrows used for daily or seasonal refuge (COSEWIC 2007; Robson 2011; Gardiner et. al 2015; Buchanan et al. 2017; Edkins 2017). Cover can also play a vital role as refuge from biotic threats, including predation (Gardiner et al. 2015).

Canadian Reptiles

Challenges faced by individuals differ between the core and periphery of their native range (Vanek and Wasko 2017). Differences in resource use (Vanek and Wasko 2017), food availability (Ferguson and McLoughlin 2000), body size (Greaves and Litzgus 2009; Marchand et al. 2018), and external conditions (Sanford et al. 2006) create additional challenges for those living at their range limits. Terrestrial reptiles in Canada are located at their northern range limits (Lesbarrères et al. 2014; COSEWIC 2019) and must deal with a thermally challenging climate (Gardiner et al. 2015). Daily temperature extremes, geographic climate differences, and seasonal extremes are common in the northern temperate region (Gardiner et al. 2015), adding additional pressures for ectotherms to effectively thermoregulate and survive. Snakes deal with thermoregulatory stress by seeking habitats with high thermal quality, such that thermal quality is a consistent variable to predicting microhabitat selection (Robertson and Weatherhead 1992; Blouin-Demers and Weatherhead 2001b; Row and Blouin-Demers 2006b; Shoemaker and Gibbs 2010).

Challenges associated with thermoregulation are not the only threats to reptiles in Canada. Over three quarters of Canada's reptile species are listed as at risk of extinction, largely due to anthropogenically-induced threats (Lesbarrères et al. 2014; COSEWIC 2019). Impacts of increased urban sprawl, resource-exploitation, and land-use changes threaten inhabitants of northern latitudes (Sala et al. 2000; Walther et al. 2002; Lesbarrères et al. 2014). Canada's altered landscape largely reflects a resource-based economy (Coristine and Kerr 2011; Lesbarrères et al. 2014), with intensive agriculture in particular, as a prominent threat to reptile diversity and critical habitat availability (Ribeiro et al. 2009). Most of the human population in Canada is concentrated in its southern regions (Statistics Canada 2008), also generating areas of intense anthropogenic activity (Kerr and Cihlar 2003). Southern regions are also some of the most diverse areas for Canadian herpetofauna (Lesbarrères et al. 2014; COSEWIC 2019); therefore, creating conflict between the demands of humans and conservation of herpetofauna.

Reptiles of Ontario

Ontario has the greatest diversity of reptile species among the Canadian provinces (COSSARO 2019; Ontario Nature 2019). However, all 8 of its turtle species and over half of its 17 snake species are listed at-risk (OMNRF 2016b; COSEWIC 2019; Ontario Nature 2019), due to road mortality and other anthropogenic impacts that have resulted in severe loss, fragmentation, and degradation of remaining suitable habitat (Crowley and Brooks 2005). As anthropogenic activity spreads further into reptile habitat, the probability of human-reptile conflict increases. Urbanization and other anthropogenic activities bring with them the need to convert natural spaces and generate roads and infrastructure, thus creating barriers, altering movements (Row et al. 2007; Robson 2011), causing direct mortality (Row et al. 2007; Rouse et al. 2011; Fortney et al. 2012; Secco et al. 2014) and local population declines (Row et al. 2007). For example, some species are known to avoid converted areas like crop fields, thus influencing their space use and habitat selection (Durner and Gates 1993; Robson 2011). However, habitat selection at the population level may vary, rendering it important to examine these requirements amongst multiple populations.

Like most Canadian provinces, Ontario's highest human population density is in the south (Statistics Canada 2008 & 2017; OMF 2019) and close to 90% of Ontario residents reside in the southern half of the province (OMF 2019). It is projected in the next 30 years that Ontario's population will grow by nearly 40%, with most of this growth in southern Ontario (OMF 2019), increasing the prevalence of habitat loss for wildlife and species at risk (Ontario Biodiversity Council 2011). Habitat loss is a primary threat to biodiversity in southern Ontario, an area that is home to some of the most biologically unique areas in the province (Ontario Biodiversity Council 2011). This uniqueness also makes it one of the most vulnerable to the effects of anthropogenic activity (Ontario Biodiversity Council 2011). The Lake Simcoe-Rideau (LSR) ecoregion in southern Ontario is one example, possessing most of Ontario's alvar habitats, a globally, federally, and provincially imperiled habitat type (OMNR 2013; OMNRF 2018). Being the second densest human-populated ecoregion in the province (OMNRF 2018), with over 57% of its land cover used for agriculture (OMNRF 2018), the threat of anthropogenic disturbance remains high. Situated in the LSR ecoregion, Huron County is one such example where widespread agricultural activity challenges the biodiversity and persistence of its flora and fauna, including reptile species-at-risk such as the eastern hog-nosed snake (*Heterodon platirhinos*; OMNRF 2018; COSSARO 2019).

The eastern hog-nosed snake is an example of one species in Ontario that has populations living amongst anthropogenically-altered environments. The eastern hog-nosed snake is a thick-bodied oviparous colubrid, which at maturity averages 50-115 cm in total length (Harding 1997; COSEWIC 2007). Like other members of the *Heterodon* genus, *H. platirhinos* is well known for its distinctive keeled snout, used for burrowing and/or nest excavation (Harding 1997; Cunnington and Cebek 2005; COSEWIC 2007). The species is also known for their charismatic defensive behaviours, by demonstrating cobra mimicry through hissing, ‘mock-striking’, and flattening the neck region, and/or flipping over dorsally to ‘feign death’ (Harding 1997; COSEWIC 2007). This provincially and federally threatened snake reaches its northern range limit in Ontario where it occurs at low densities (COSEWIC 2007; OMNRF 2016b; COSEWIC 2021), predominantly limited to densely human-populated portions of southern Ontario (COSEWIC 2007). Like many of Ontario’s snakes, eastern hog-nosed snakes are cryptic and difficult to survey (OMNRF 2016b), and little is known about their ecology and life history. However, knowledge of their distribution, population sizes, spatial ecology, habitat preferences, and life history are imperative to meeting government mandated recovery actions (OMNRF 2016a) to improve their status and ensure their persistence in Ontario. This study aims to address these knowledge gaps in a recently reported population of hog-nosed snakes living amongst anthropogenic activity in southwestern Ontario, by studying their spatial ecology and habitat preferences, and by assessing potential threats.

Literature Cited

Aebischer, N.J., Robertson, P.A., and Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology **74**: 1313-1325.

Alford, R.A. and Richards, S.J. 1999. Global amphibian declines: A problem in applied ecology. Annual Review of Ecology and Systematics **30**: 133-165.

Aragon, P., Lobo, J.M., Olalla-Tarrage, M.A., and Rodriguez, M.A. 2010. The contribution of contemporary climate to ectothermic and endothermic vertebrate distributions in a glacial refuge. Global Ecology and Biogeography **19**: 40-49.

Ashley, P.E., Kosloski, A., and Petrie, S.A. 2007. Incidence of intentional vehicle-reptile collisions. Human Dimensions of Wildlife **12**(3): 137-143.

Blouin-Demers, G., and Weatherhead, P.J. 2001a. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes *Elaphe obsoleta obsoleta*. Journal of Animal Ecology **70**: 1006-1013.

Blouin-Demers, G. and Weatherhead, P.J. 2001b. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology **82**: 3025-3043.

Blouin-Demers, G., and Weatherhead, P.J. 2002. Habitat-specific behavioral thermoregulation by black rat snakes (*Elaphe o. obsoleta*). Oikos **97**: 59-68.

Blouin-Demers, G. and Nadeau, P. 2005. The cost-benefit model of thermoregulation does not predict lizard thermoregulatory behavior. Ecology **86**(3): 560-566.

Blouin-Demers, G., and Weatherhead, P.J. 2008. Habitat use is linked to components of fitness through the temperature-dependence of performance in ratsnakes (*Elaphe obsoleta*). Israel Journal of Ecology and Evolution **54**: 361-372.

Boggie, M.A. and Mannan, R.W. 2014. Examining seasonal patterns of space use to gauge how and accipiter responds to urbanization. Landscape and Urban Planning **124**: 34-42.

Bolton, R.M., and Brooks, R.J. 2010. Impact of the seasonal invasion of *Phragmites australis* (common reed) on turtle reproductive success. Chelonian Conservation and Biology **9**(2): 238-243.

Buchanan, S.W., Timm, B.C., Cook, R.P., Couse, R., and Hazard, L.C. 2017. Spatial ecology and habitat selection of eastern hognose snakes. Journal of Wildlife Management **81**(3): 509-520.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy **24**(3): 346-352.

Buskirk, S.W., and Millspaugh, J.J. 2006. Metrics for studies of resources selection. Journal of Wildlife Management **70**(2): 358-366.

Congdon, J.D., Dunham, A.E., and Van Loben Sels, R.C. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conservation Biology **7**(4): 826-833.

Congdon, J.D., Dunham, A.E., van Loben Sels, R.C. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): Implications for conservation and management of long-lived organisms. American Zoologist **34**: 397-408.

Cook, C.E., McCluskey, A.M., and Chambers R.M. 2018. Impacts of invasive *Phragmites australis* on diamondback terrapin nesting in Chesapeake Bay. Estuaries and Coasts **41**: 966-973.

Coristine, L.E. and Kerr, J.T. 2011. Habitat loss, climate change, and emerging conservation challenges in Canada. Canadian Journal of Zoology **89**: 435-451.

COSEWIC. 2007. COSEWIC Assessment and Update Status Report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. viii + 36 pp.

COSEWIC. 2019. Committee on the Status of Endangered Wildlife in Canada. Available from: http://www.cosewic.ca/index.php/en-ca/ [Accessed 20 November 2019].

COSEWIC. 2021. COSEWIC Assessment and Update Status Report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xi + 45 pp.

COSSARO. 2019. Species. Available from: http://cossaroagency.ca/species/ [Accessed 30 October 2019].

Crowley, J.F. and Brooks, R.J. 2005. Protected Areas and the Conservation of Ontario's Reptile Species at Risk: Safe Havens or False Hopes? *In* Proceedings of the Parks Research Forum of Ontario State-of-the-Art Workshop series #2, Peterborough, ON., 11-13 January 2005. Parks Research Forum of Ontario, Waterloo, ON. pp. 139-152.

Cummins, E. 2019. Rattlesnake roundups are a southern tradition. They're also an ecological disaster. Available from: https://www.popsci.com/rattlesnake-roundup-ecology-gassing/ [Accessed 30 October 2019].

Cunnington, G.M. and Cebek, J.E. 2005. Mating and nesting behavior of the eastern hognose snake (*Heterodon platirhinos*) in the northern portion of its range. American Midland Naturalist **154**(2): 474-478.

Durner, G.M., and Gates, J.E. 1993. Spatial ecology of black rat snakes on Remington Farms, Maryland. Journal of Wildlife Management **57**(4): 812-826.

Dzialowski, E.M. 2005. Use of operative temperature and standard operative temperature models in thermal biology. Journal of Thermal Biology **30**: 317-334.

Edkins, T.L. 2017. Variable habitat selection and space use among bullsnake (*Pituophis catenifer sayi*) populations: distance between seasonal habitats drives space use. M.Sc. Thesis, Biology, University of Regina, Regina, Saskatchewan.

Ettling, J.A., Aghasyan, L.A., Aghasyan, A.L., and Parker, P.G. 2013. Spatial ecology of Armenian vipers, *Montivipera raddei*, in a human-modified landscape. Copeia **2013**: 64-71.

Ettling, J.A., Aghasyan, L.A., Aghasyan, A.L., and Parker, P.G. 2016. Spatial ecology of Armenian vipers, *Montivipera raddei*, in two different landscapes: human-modified vs. recovered natural. Russian Journal of Herpetology **23**(2): 93-102.

Ferguson, S.H. and McLoughlin, P.D. 2000. Effect of energy availability, seasonality, and geographic range on brown bear life history. Ecography **23**: 193-200.

Fitch, H.S. 1998. The Sharon Springs roundup and prairie rattlesnake demography. Transactions of the Kansas Academy of Science **101**(3-4): 101-113.

Fortney, A.N., Poulin, R.G., Martino, J.A., Parker, D.L., and Somers, C.M. 2012. Proximity to hibernacula and road type influence potential road mortality of snakes in southwestern Saskatchewan. Canadian Field Naturalist **126**(3): 194-203.

Gardiner, L.E., Somers, C.M., Parker, D.L., and Poulin, R.G. 2015. Microhabitat selection by prairie rattlesnakes (*Crotalus viridis*) at the northern extreme of their geographic range. Journal of Herpetology **49**(1): 131-137.

Gans, C., and Pough, H.F. (Eds.) 1982. Biology of the Reptilia, Volume 13, Physiology D: Physiological Ecology. Academic Press, London, New York, Paris, San Diego, San Francisco, São Paulo, Sydney, Tokyo, and Toronto xiii + 345 pp.
Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., and Winne, C.T. 2000. The global decline of reptiles, déjà vu amphibians. BioScience **50**(8): 653-666.
Gill, D.E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs **48**: 145-166.
Greaves, W.F., and Litzgus, J.D. 2009. Variation in life-history characteristics among populations of North American wood turtles: a view from the north. Journal of Zoology **279**(3): 298-309.
Grover, M.C. 1996. Microhabitat use and thermal ecology of two narrowly sympatric *Sceloporus* (Phrynosomatidae) lizards. Journal of Herpetology **30**: 152-160.
Harding, J.H. 1997. Amphibians and Reptiles of the Great Lakes Region. University of Michigan Press, Ann Arbor, MI. 378 pp.
Hecnar, S.J. 1997. Amphibian Pond Communities in Southwestern Ontario. *In* Amphibians in Decline: Canadian Studies of Global Phenomenon, D.M. Green (ed.). Herpetological Conservation **1**: 1-15.
Heisler, L.M., Somers, C.M., Wellicome, T.I., and Poulin, R.G. 2013 Landscape-scale features affecting small mammal assemblages on the northern Great Plains of North America. Journal of Mammalogy **94**(5): 1059-1067.
Hertz, P.E., Huey, R.B., and Stevenson, R.D. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. The American Naturalist **142**: 796-818.
Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M., and Williams, S.E. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philosophical Transactions of the Royal Society B: Biological Sciences **367**: 1665-1679.
Huey, R.B., and Kingsolver, J.G. 1993. Evolution of resistance to high temperature in ectotherms. American Naturalist **142**: S21-S46.
Innes, R.J., Babbitt, K.J., and Kanter, J.J. 2008. Home range and movement of Blanding's turtles (*Emydoidea blandingii*) in New Hampshire. Northeastern Naturalist **15**(3): 431-444.
Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, **61**(1): 65-71.
Johnson, N.B., Poulin, R.G., and Somers, C.M. 2022. Thermoregulation by bullsnakes (*Pituophis catenifer sayi*): do burrows make life easier on the prairies? Canadian Journal of Zoology: **100**(5): 303-314.
Kapfer, J.M., Doehler, K., and Hay, R. 2013. The influence of habitat type and the presence of an invasive wetland plant (*Phalaris arundinacea*) on capture rates of sympatric rare and common gartersnake species (*Thamnophis butleri* and *Thamnophis sirtalis*). Journal of Herpetology **47**(1): 126-130.
Kay, G.M., Driscoll, D.A., Lindenmayer, D.B., Pulsford, S.A., and Mortelliti, A. 2016. Pasture height and crop direction influence reptile movement in an agricultural matrix. Agriculture, Ecosystems and Environment **235**: 164-171.
Kerr, J.T. and Cihlar, J. 2003. Land use and cover with intensity of agriculture for Canada from satellite and census data. Global Ecology and Biogeography **12**(6): 161-172.

Kjoss, V.A., and Litvaitis, J.A. 2001. Community structure of snakes in a human-dominated landscape. Biological Conservation **98**(3): 285-292.

Krebs, J.R., and Davies, N.B. 1997. Behavioural Ecology: An evolutionary approach. Wiley-Blackwell, Oxford, UK.

Langley, W.M., Lipps, H.W., and Theis, J.F. 1989. Responses of Kansas motorists to snake models on a rural highway. Transactions of the Kansas Academy of Science **92**(1/2): 43

Lelièvre, H.G., Blouin-Demers, G., Bonnet, X., and Lourdais, O. 2010. Thermal benefits of artificial shelters in snakes: A radiotelemetric study of two sympatric colubrids. Journal of Thermal Biology **35**: 324-331.

Lelièvre, H.G., Blouin-Demers, G., Pinaud, D., Lisse, H., Bonnet, X., and Lourdais, O. 2011. Contrasted thermal preferences translate into divergences in habitat use and realized performance in two sympatric snakes. Journal of Zoology **284**: 265-275.

Lesbarrères, D., Ashpole, S.L., Bishop, C.A., Blouin-Demers, G., Brooks, R.J., Echaubard, P., Govindarajulu, P., Green, D.M., Hecnar, S.J., Herman, T., Houlahan, J., Litzgus, J.D., Mazerolle, M.J., Paszkowski, C.A., Rutherford, P., Schock, D.M., Storey, K.B., and Lougheed, S.C. 2014. Conservation of herpetofauna in northern landscapes: threats and challenges from a Canadian perspective. Biological Conservation **170**: 48-55.

Lienart, G.D.H., Mitchell, M.D., Ferrari, M.C.O., and McCormick, M.I. 2014. Temperature and food availability affect risk assessment in an ectotherm. Animal Behaviour **89**: 199-204.

Lovich, J.E., Ennen, J.R., Agha, M., and Gibbons, J.W. 2018. Where have all the turtles gone and why does it matter? BioScience **68**(10): 771-781.

Marchand, K.A., Hughes, G.N., and Litzgus, J.D. 2018. Geographic variation in somatic growth rate of wood turtles (*Glyptemys insculpta*). Copeia **106**(3): 477-484.

Markle, C.E., and Chow-Fraser, P. 2018. Effects of European common reed on Blandling's turtle spatial ecology. Journal of Wildlife Management **82**(4): 857-864.

Markle, C.E., Chow-Fraser, G., and Chow-Fraser, P. 2018. Long-term habitat changes in a protected area: Implications for herpetofauna habitat management and restoration. PLoS ONE **13**(2): 1-15.

Maron, D.F. 2019. Turtles are being snatched from U.S. waters and illegally shipped to Asia. Available from: https://www.nationalgeographic.com/animals/2019/10/american-turtles-poached-to-become-asian-pets/ [Accessed 30 October 2019].

Marshall, B.M., Strine, C.T., Jones, M.D., Theodorou, A., Amber, E., Waengsothorn, S., Suwanwaree, P., and Goode, M. 2018. Hits close to home: repeated persecution of king cobras (*Ophiophagus hannah*) in northeastern Thailand. Tropical Conservation Science **11**: 1-14.

Maslow, A.H. 1943. A theory of human motivation. Psychological Review **50**: 370-396.

Mattison, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G.R., and Pedersen, H.C. 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia **173**: 813-825.

Meffe, G.K., and Carroll, R.C. 1997. Principles of Conservation Biology. 2nd ed. Sinauer Associates Inc., Sunderland, Massachusetts. 729 pp.

Moorter, B.V., Rolandsen, C.M., Basille, M., and Gaillard, J.M. 2016. Movement is the glue connecting home ranges and habitat selection. Journal of Animal Ecology **85**: 21-31.

National Wildlife Federation. 2019. Invasive Species. Available from: https://www.nwf.org/Educational-Resources/Wildlife-Guide/Threats-to-Wildlife/Invasive-Species [Accessed 20 October 2019].

Okarma, H., Jędrzejewski, W., Schmidt, K., Śnieżko, S., Bunevich, A.N., and Jędrzejewska, B. 1998. Home ranges of wolves in Bialowieża Primeval Forest, Poland compared with other Eurasian populations. Journal of Mammalogy **79**(3): 842-852.

OMF. 2019. Ontario Population Projections, 2018-2046. Ontario Ministry of Finance, Office of Economic Policy. Toronto, ON. ii + 109 pp.

OMNR. 2011. Invasive *Phragmites*—Best Management Practices. Ontario Ministry of Natural Resources. Peterborough, ON. Version 2011. 15pp.

OMNR. 2013. Recovery Strategy for the Lakeside Daisy (*Tetraneuris herbacea*) in Ontario. Adoption of the Recovery Strategy for the Lakeside Daisy (*Hymenoxys herbacea*) in Canada (Parks Canada Agency 2011). Ontario Ministry of Natural Resources, Peterborough, ON. iii + 5 pp + Appendix xi + 60 pp.

OMNRF. 2016a. Eastern Hog-nosed Snake Government Response Statement. Ontario Ministry of Natural Resources and Forestry, Species Conservation Policy Branch. Peterborough, ON. 6 pp.

OMNRF. 2016b. Survey Protocol for Ontario's Species at Risk Snakes. Ontario Ministry of Natural Resources and Forestry, Species Conservation Policy Branch. Peterborough, ON. ii + 17 pp.

OMNRF. 2018. The Ecosystems of Ontario—Part 1: Ecozones and Ecoregions. Available from: https://www.ontario.ca/page/ecosystems-ontario-part-1-ecozones-and-ecoregions [Accessed 27 November 2019].

Ontario Biodiversity Council. 2011. Ontario's Biodiversity Strategy, 2011: Renewing Our Commitment to Protecting What Sustains Us. Ontario Biodiversity Council, Peterborough, ON. vi + 69 pp.

Ontario Nature. 2019. Reptiles and Amphibians. Available from: https://ontarionature.org/programs/citizen-science/reptile-amphibian-atlas/species/ [Accessed 13 October 2019].

Pike, D.A., Croak, B.M., Webb, J.K., and Shine, R. 2010. Subtle – but easily reversible – anthropogenic disturbance seriously degrades habitat quality for rock-dwelling reptiles. Animal Conservation **13**: 411-418.

Reinert, H.K. 1993. Habitat selection in snakes. *In* Snakes: Ecology and Behaviour. *Edited by* R.A. Seigel & J.T. Collins, The Blackburn Press, Caldwell. pp. 201-240.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F., and Hirota, M. 2009. The Brazilian Atlantic forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation **142**: 1141-1153.

Robertson, I.C., and Weatherhead, P.J. 1992. The role of temperature in microhabitat selection by northern water snakes (*Nerodia sipedon*). Canadian Journal of Zoology **70**: 417-422.

Robson, L.E. 2011. The spatial ecology of eastern hognose snakes *(Heterodon platirhinos*): habitat selection, home range size, and the effect of roads on movement patterns. M.Sc. thesis, Biology, University of Ottawa, Ottawa, Ontario.

Rotem, G. and Ziv, Y. 2016. Crop diversity and rotation may increase dispersal opportunities of reptiles in a heterogeneous agroecosystem. Agriculture, Ecosystems & Environment **235**(1): 32-37.

Rouse, J.D., Wilson, R.J., Black, R., and Brooks, R.J. 2011. Movement and spatial dispersion of *Sisturus catenatus* and *Heterodon platirhinos*: Implications for interactions with roads. Copeia **2011**(3): 443-456.

Row, J.R. and Blouin-Demers, G. 2006a. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. Ecoscience **13**(4): 443-450.

Row, J.R. and Blouin-Demers, G. 2006b. Thermal quality influence effectiveness of thermoregulation, habitat use, and behaviour in milk snakes. Oecologia **148**: 1-11.

Row, J.R., Blouin-Demers, G., and Weatherhead, P. 2007. Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). Biological Conservation **137**(1): 117-124.

Sanford, E., Holzman, S.B., Rand, D.M., and Bertness, M.D. 2006. Larval tolerance, gene flow, and the northern geographic range limit of fiddler crabs. Ecology **87**: 2882-2894.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., and Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. Science **287**: 1770-1774.

Seburn, D., and Seburn, C. 2000. Conservation priorities for the amphibians and reptiles of Canada. World Wildlife Fund Canada and Canadian Amphibian and Reptile Conservation Network, Toronto, ON and Delta, BC. v + 93 pp.

Secco, H., Ratton, P., Castro, E., da Silva Lucas, P., and Bager, A. 2014. Intentional snake road-kill: a case study using fake snakes on a Brazilian road. Tropical Conservation Science **7**(3): 561-571.

Shine, R., Webb, J.K., Fitzgerald, M., and Summer, J. 1998. The impact of bush-rock removal on an endangered species, *Hoplocephalus bungaroides* (Serpentes: Elapidae). Wildlife Research **25**: 285-295.

Shoemaker, K.T., and Gibbs, J.P. 2010. Evaluating basking-habitat deficiency in the threatened eastern massasauga rattlesnake. Journal of Wildlife Management **74**: 504-513.

Smith, M.A., and Green, D.M. 2005. Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography **28**: 110-128.

Statistics Canada. 2008. Canadian Demographics at a Glance. Catalogue no. 91-003-XIE. Statistics Canada, Government of Canada.

Statistics Canada. 2017. Population Size and Growth in Canada: Key Results from the 2016 Census. Statistics Canada Catalogue no. 11-001-X. Statistics Canada, Government of Canada, Ottawa.

Thorpe, S.J., and Salkovskis, P.M. 1997. Animal Phobias *In* Phobias: A handbook of theory, research, and treatment. *Edited by* G.C.L. Davey. Wiley, Chichester, UK. pp: 81-106.

Todd, B.D., Willson, J.D., and Gibbons, J.W. 2010. The Global Status of Reptiles and Causes of their Decline *In* Ecotoxicology of Amphibians and Reptiles, second edition. *Edited by* D.W. Sparling, C.A. Bishop, and S. Krest. CRC Press, Pensacola, FL. pp. 47-67.

Vanek, J.P., and Wasko, D.K. 2017. Spatial ecology of the eastern hog-nosed snake (*Heterodon platirhinos*) at the northeastern limit of its range. Herpetological Conservation and Biology **12**: 109-118.

Waldschmidt, S., and Tracy, C.R. 1983. Interactions between a lizard and its thermal environment: implications for sprint performance and space utilization in the lizard *Uta stansburiana*. Ecology **64**(3): 476-484.

Walkup, D.K., Leavitt, D.J., and Fitzgerald, L.A. 2017. Effects of habitat fragmentation on population structure of dune-dwelling lizards. Ecosphere **8(3**): 1-14.
Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. Nature **416**: 389-395.
Wolf, A.J., Hellgren, E.C., III Bogosian, V., and Moody, R.W. 2013. Effects of habitat disturbance on Texas horned lizards: an urban case study. Herpetologica **69**(3): 265-281.
Yorek, N. 2009. The only good snake is a dead snake: secondary school students' attitudes toward snakes. Biotechnology & Biotechnological Equipment **23**(1): 31-35.

Chapter 1: EVALUATING THE SPATIAL ECOLOGY OF A POPULATION OF EASTERN HOG-NOSED SNAKES IN AN AGRICULTURAL LANDSCAPE

Abstract

Basic information lacks for many reptile species, although understanding aspects such as space use and habitat preferences can be crucial to conserving at-risk populations. The eastern hog-nosed snake (*Heterodon platirhinos*) is listed as Threatened in Ontario. Little is known about the ecology and life history of the species in Ontario, although such information is required to meet government-mandated recovery actions and conserve local critical habitat. I investigated whether putatively higher chances of anthropogenic interaction influenced spatial ecology of hog-nosed snakes in a human-modified landscape in Huron County, southwestern Ontario. I recorded general habitat selection and space use (mean ± SD) during the active seasons of 2018 to 2020 for ten individuals radio-tracked 2-5x/week. Snakes had a mean of 127 ± 41 m per movement, 49 ± 13 m per day, and moved within a mean home range size of 64 ± 30 ha. Beach, forest, and old field habitats were preferred at landscape and home-range scales, while anthropogenic, bluff, cropland, and riparian habitats were avoided. While pockets of natural habitat exist, anthropogenic activity is widespread across the study site and appears to negatively impact eastern hog-nosed snake spatial ecology. Human modified areas also influence movement in Huron County; compared to other North American populations, Huron County snakes moved greater distances per day within larger-sized home ranges. A diversity of competing land uses presents a unique suite of threats for this population of eastern hog-nosed snakes in Huron County. As a result of these threats, snake spatial ecology must be considered by government and conservation agencies when drafting and implementing management plans to ensure the species persists in Huron County.

Introduction

Herpetofauna are among the oldest extant terrestrial vertebrates, yet globally over 50% of reptile and amphibian species are currently threatened with extinction (Gibbons et al. 2000; Lesbarrères et al. 2014; WWF 2016). Basic information is lacking for many reptile species, presenting challenges for assessing conservation status and creating effective recovery plans to mitigate global declines (Seburn and Seburn 2000; Bohm et al. 2013). A combination of factors, including difficulties with detection and radio transmitter attachment has led to knowledge gaps in population size estimates and basic biological data for many reptiles (Parker and Plummer 1987; Seburn and Seburn 2000; Lesbarrères et al. 2014; Griffiths et al. 2015).

Understanding spatial ecology is a crucial component of effective species-at-risk recovery strategies, yet for many reptile species, aspects of their spatial ecology are currently unknown (Buchanan et al. 2017). Spatial ecology studies include assessing habitat use and selection, estimating home range sizes, and identifying movement patterns (Millar and Blouin-Demers 2011). For reptile species inhabiting areas with anthropogenic activity, studying space use can be complex. Anthropogenic disturbance can influence movement patterns, leading to reduced movement frequency, shorter movement distances, and area avoidance (Parent and Weatherhead 2000; Kwiatkowsi et al. 2008; Corey and Doody 2010; Beale et al. 2016) or increased movement frequency, distance, and area use (Kerr et al. 2004a and 2004b; Millar and Blouin-Demers 2011; Beale et al. 2016; Edkins 2017; Zagorski et al. 2019). These responses to anthropogenic activity can affect fitness by interfering with mate dispersion and nesting behaviour, causing reduced fecundity, and increasing mortality (Parent and Weatherhead 2000; Moore and Seigel 2006; Szerlag-Egger and McRobert 2007; Jenkins et al. 2009; Rouse et al. 2011; Yang et al. 2017).

A population of eastern hog-nosed snakes (*Heterodon platirhinos*) was reported in 2011 in the agriculturally-dominated landscape of Huron County, Ontario (Huron Stewardship Council unpublished data; Duhatschek 2018). Eastern hog-nosed snakes are known for their dramatic defensive behaviours, either demonstrating cobra mimicry by hissing, ‘mock-striking’, and flattening the neck region, and/or flipping over dorsally and ‘feigning death’ (Harding 1997; COSEWIC 2007). Despite their charismatic nature, they are cryptic in their behaviour, making them difficult to survey. The species is listed as Threatened in Ontario (OMNRF 2019), and top priority recovery actions for the species include describing its habitat selection and home range (Kraus 2011; OMNRF 2016a). Although the spatial ecology of eastern hog-nosed snakes has previously been examined at the northern edge of their range (Cunnington 2004; Robson 2011; Buchanan et al. 2017; Vanek and Wasko 2017), space use by Huron County snakes may differ, as space use can generally vary among snake populations (Smith et al. 2015; Ettling et al. 2016; Edkins 2017) and be impacted by different habitat modifications (Parent and Weatherhead 2000; Kwiatkowsi et al. 2008; Beale et al. 2016). Eastern hog-nosed snakes are considered highly mobile, moving ~100 m in a day (Cunnington 2004), travelling over 5 km throughout an active season (Rouse 2006), and having home ranges that surpass 100 ha (Cunnington 2004). But compared to other Ontario snake species-at-risk, eastern hog-nosed snakes have a low detection probability because of their cryptic behaviour, spending large portions of their time out of view/inaccessible to surveyors (Ford et al. 1991; Fitch 1993; Ernst and Ernst 2003; OMNRF 2016b). Consequently, there is a lack of basic information about this species, even though such information is vital to managing and conserving it in Ontario (OMNRF 2016a, 2016b, 2019).

Hypothesis and Predictions

I hypothesized that because the eastern hog-nosed snake population in Huron County is located in a highly modified area, the distribution, home range size, and habitat selection of its individuals would differ from those in other populations in less impacted areas of Ontario. I predicted that:

1. Movement and general habitat selection would reflect avoidance of heavily modified areas.
2. Distances moved would be greater than in other populations, as individuals in Huron County would have to move farther and wider to avoid human activity while seeking out resources.

Materials & Methods

Study Site

Data were collected in Huron County, Ontario, Canada (Latitude: 43° 38' 41", Longitude: -81° 41' 25"). The area is within the mixed-wood plains ecozone (OMNRF 2018) with vegetation communities influenced by two major water systems: the Maitland River and Lake Huron. Agriculture, tourism, and seasonal lakeshore activity largely drive the local economy as a result of the predominantly sandy lakeshore, clay till soils, and suitable soils for agriculture (Hoffman et. al 1952; Cummings et al. 1998; OMNRF 2018). The area consists of a diversity of habitat types including cropland, anthropogenic infrastructure (e.g., small municipal airport, marina), and natural areas including steep lakeside bluffs, forest, the Lake Huron shoreline, and other habitat types (i.e., old field, riparian, juniper shrubland) interspersed between (Table 1.1, 1.2; Fig. 1.1). Although much of the area atop the lakeshore bluff has been cleared for seasonal and permanent residences, shoreline and river valley infrastructure is of low density and most of the bluff is experiencing ongoing natural erosion activity.

Study Species

The eastern hog-nosed snake is endemic to North America, with their core range in the eastern United States, and northern extent of their distribution in Ontario, Canada (Conant and Collins 1998; COSEWIC 2007; Robson 2011). Extant Canadian populations are limited to southern Ontario, occurring as two geographically separate populations: those found in south-central Ontario from Georgian Bay to Peterborough, and populations found in the Carolinian forests of southwestern Ontario (Robson 2011; COSEWIC 2021). The distribution of *H. platirhinos* is limited by the need for sandy soils to dig nests for egg incubation (Michener and Lazell 1989; Cunnington and Cebek 2005; COSEWIC 2007). The species is listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as Threatened, due to habitat loss, habitat fragmentation, and human persecution (Seburn 2009; COSEWIC 2021).

Mark-Recapture Surveys and Radio-telemetry

Visual encounter surveys (VES) and radio telemetry were the primary methods used to actively survey for snakes over 3 field seasons (2018 – 2020). Daily VES began around expected time of emergence from hibernation in mid-April and while following snake species-at-risk survey protocols (>10 surveys in an active season; OMNRF 2016b). Generally, a team of 1 to 2 surveyors conducted VES 4 – 7 times per week and were concentrated in areas with previously reported sightings, as well as areas of suitable habitat (i.e., dune and forested areas; OMNRF 2016b). Searches for snakes included walking within suitable habitat when air temperature was between 10 and 30°C (Casper et al. 2001; EMRT 2005; Harvey 2008) and simultaneously examining the ground surface, as well as amongst and beneath potential cover objects (e.g., shrub, driftwood; OMNRF 2016b). As vegetation became denser and telemetry work increased, VES effort became less frequent. However, by late June/early July around the expected nesting period, VES search effort increased in the area known to have nesting activity previously identified by the Huron Stewardship Council (unpublished report, Huron Stewardship Council). Focusing search in this area allowed recording the occurrence of any females not previously captured. Nesting search efforts occurred earlier and later in the day when temperatures were slightly cooler (sunrise to 09:00 and 17:00 to sunset), in an attempt to coincide with optimal mean temperature for nesting by *H. platirhinos* (24°C; Peet-Paré and Blouin-Demers 2012).

As the study area contained residential buildings and roads, surveys near these anthropogenic features were useful for targeting snakes crossing or having been killed on roads. One to three times a week, main roads were walked or driven slowly (not exceeding 45 km/h; Langen et al. 2007; Sullivan 2012; OMNRF 2016b), recording upon observation of a snake, whether it was alive or dead, the location, and its behaviour if alive. Eight plywood coverboards (approximately 1 m x 0.5 m sized) were also placed 20 m to 50 m apart throughout fallow airport fields in an attempt to capture snakes seeking refuge in areas cleared for aircraft use. For a species recognized as being cryptic and largely spending time under refugia, coverboards were intended to help increase the probability of detecting snakes in this open area (Halliday and Blouin-Demers 2015; OMNRF 2016b). Initially, the boards were to be checked 2-3x/week, but after reflecting upon the lack of use of the airport area and lack of use of the coverboards by telemetered snakes in 2018, coverboards were instead checked bi-weekly in 2019 and 2020.

Active and passive methods were used to identify, locate, and track movements of individuals. Mark-recapture was used to identify new or previously caught individuals. For individual identification, newly captured individuals >30 g were subcutaneously implanted with a Passive Integrated Transponder (PIT) tag (Leuenberger et al. 2019). A syringe injector was used to insert a PIT tag within the lower third of the venter and anterior to the cloacal scales (Leuenberger et al. 2019). Morphometric measurements were recorded for new individuals and snakes recaptured at the start of each active season. Morphometrics measured included: snout-vent length (SVL), tail length (TL), mass (g), and sex (based on probing; Schaefer 1934). Radio telemetry was used to monitor the spatial ecology of a subset of the population. Programmable radio transmitters (Sigma8, Aurora, Ontario) were surgically implanted by a veterinarian into the body cavities of subadult and adult, non-gravid (at the time of implantation) females and males. To comply with the maximum transmitter mass to body mass ratio of 0.05:1 dictated by our animal care protocol, radio transmitters (I-450 Model, mass = 8.5 g) were only implanted in snakes with a mass >200 g. Radio transmitters were programmed to run 08:00-20:00 for the anticipated active season from 1 April to 1 November, and to reactivate for a week in January to confirm hibernaculum sites. Surgical procedures were completed by Dr. Sean Egan (Egan-Fife Animal Hospital, Chatham, Ontario), approved under AUP #19-386, and followed snake surgical procedures outlined by Wilson (2004) and Crawshaw and Lentini (2013). Post-surgery, snakes were held and observed for 48 hours before release at original capture locations.

Snakes implanted with transmitters were tracked 2-5 x/week throughout the active season using a Yagi-antenna and an Advanced Telemetry Systems (ATS) receiver (4 MHz frequency range; Model R410; Isanti, Minnesota). At each observation, we recorded 1) GPS coordinates of location, 2) date and time, 3) behaviour, 4) general habitat type, 5) air and ground temperatures (°C), and 6) weather (precipitation, cloud cover based on four increments between 0-100%). Location coordinates were collected using Survey123 (ESRI 2021) on a Samsung Galaxy tablet equipped with a GPS amplifier (EOS Tools Pro; ±1 m accuracy). Snake movement > 1 m from a previously observed location was considered movement to a 'new' location; a minimum of >1 m took into account small snake movements and acted as a buffer for potential GPS accuracy error.

Home Ranges and Movements

Spatial analyses included data I recorded in 2019 and 2020, as well as data collected from snakes caught and/or tracked in 2017 and 2018 by Huron Stewardship Council (HSC) staff (Maddalena 2019). I used the 'adehabitat' R package (Calenge 2006) to analyze snake spatial ecology. For individuals tracked most of an entire active season (between 1 April and 1 November), home range sizes were calculated using 95% kernel density estimates (KDE; Worton 1989; Edkins 2017; Vanek and Wasko 2017) and 95% and 50% minimum convex polygons (MCP; Calenge 2006; Moore and Gillingham 2006; Sutton et al. 2017; Vanek and Wasko 2017). Although MCP is the most commonly used analysis and includes all observations, it fails to acknowledge spatial and temporal selection patterns and incorporates unused areas (Hansteen et al. 1997; Burgman and Fox 2003; Nilsen et al. 2008; Robson 2011). Kernels acknowledge spatiotemporal patterns and weigh intensely-used areas more heavily (Row and Blouin-Demers 2006c; Robson 2011). To compare methods and get the most realistic depictions of home ranges, I used both MCP and KDE (Row and Blouin-Demers 2006a). For individuals not tracked for a full active season, home range size (y-axis) was plotted against number of radio-locations (x-axis; Fig. 1.2; Row and Blouin-Demers 2006b; Boyle et al. 2009; Maddalena 2019) to determine whether an individual used their entire home range; use of entire home range was assumed when the relationship approached an asymptote (Fig. 1.2). Snakes for whom there were not enough location points to reach asymptote were not included in home range analyses.

I examined active season (April – October), seasonal (e.g., monthly) and sex-specific movements patterns. I calculated distance moved per day (DPD; mean ± SD) and per movement (DPM; mean ± SD) of all radio-tracked individuals (Row et al. 2007; Sutton et al. 2017; Maddalena 2019). DPM was calculated as the mean of all sequential distances from a location that an individual moved (>1 m distance); locations from where an individual did not move (<1 m distance) were disregarded. DPD was calculated by dividing distance moved between two sequential radio locations by the number of days between those two radio locations. To determine whether the movement data were auto-correlated, and whether DPM and DPD were dependent on previous snake observation locations (Neyman 1934), movement data for each snake were analyzed using the auto-correlation function (acf) in R. Generalized linear mixed models (GLMMs; Bates et al. 2015) were then used to test if movement data were influenced by seasonal effects with month (fixed effect; April through to October) and individual ID (random effect) modelled under a Gaussian distribution. To test for the influence of sex effects on DPM and DPD by month, I performed one-way ANOVAs (Analysis of Variance) where DPD and DPM were modelled as functions of sex (fixed effect) in each month of the active season (April - October). Some females that were not gravid at time of implantation surgery would later become gravid in the same (or subsequent) year. As number of radio locations varied per snake and produced a log normal distribution for DPD and DPM, movement data were log(10) transformed prior to conducting GLMM and ANOVA analyses for DPD and DPM. Since movement patterns were expected to differ based on reproductive status (Parent and Weatherhead 2000; Buchanan et al. 2017), movements by females when gravid were initially to be treated as a separate sex category from distances by males and non-gravid females. However, when comparing movements of males, non-gravid females, and gravid females during the gravid period (June to

July), I found no significant differences (GLMM; $p > 0.05$), so movements data of gravid and non-gravid females were combined for subsequent analyses.

General Habitat Use, Selection, and Avoidance

To examine habitat selection and avoidance, I mapped and categorized the study area into 9 different habitats (Table 1.1). Aerial imagery (Huron County 2015, 0.2 m^2 resolution; CNES 2020) was used to delineate boundaries of the study area (referenced from the farthest snake radio-telemetry locations in each cardinal direction) and habitat type boundaries (divided into polygons and categorized by habitat type) within ArcMap (v.10.5.1; ESRI 2021). I then used compositional analysis (Aebischer et al. 1993; Bishir et al. 2018; Howze et al. 2019) to assess habitat selection, with each habitat type quantified as a percentage of the total study area (i.e., total area for each habitat type divided by total area of all delineated habitats combined). In ArcMap, random points within the study area boundary and within each individual's home range were created using the 'generate random points' tool to determine whether habitat selection was random or if snakes avoided certain habitat types (Laverty et al. 2016). For every radio location where a snake was detected (hereafter, location point), three random points were generated within boundaries of each habitat type and home range polygons of each snake. The distances to habitat types from location points and random points were later measured in ArcMap and compared to determine if there were significant differences between them using ANOVA (Laverty et al. 2016). A chi-square test was also used to assess if the number of location points differed by habitat type.

A resource selection function (RSF) model was created to assess the significance of habitat type (Table 1.1) in predicting snake occurrence at landscape and home range scales (Johnson 1980; Manly et al. 2002; Edge et al. 2010). The model evaluated whether snake occurrence (a binary factor) was predicted by multiple factors, distances to nine specific habitat types (from location and random points). Landscape scale included all habitat available across the study site, while home range scale polygons were calculated from minimum convex polygons (MCP) of each snake. For mapping purposes, MCP polygons for all snake home ranges that reached asymptote were digitized using the minimum bounding geometry tool (convex hull; auto-calculated at 100%) in ArcMap (ESRI 2021). In cases where pairs of predictor variable were highly correlated (Pearson correlation > 0.6), covariates were first run through univariate models and the variable that performed best based on AICc score (Akaike Information Criterion corrected for small sample sizes; Hurvich and Tsai 1989; Burnham and Anderson 2002) was kept and included in the global model. At the landscape scale, correlation coefficients between distances to beach and open sandy juniper habitats produced unacceptably high correlations, with beach the better performer in model averaging and thus retained in the global model, while at the home range scale, forest and human habitats were highly correlated. All possible predictor combinations of the global model (snake occurrence ~ habitat type) and a null (intercept) model were fitted and ranked using AICc (Hurvich and Tsai 1989; Burnham and Anderson 2002). Unconditional 85% confidence intervals (CI; Arnold 2010) and model-averaged coefficients (Barton 2019) were computed from all sub-sets of models. Only standard error and predicted values of the top-ranked AICc model were used to assess general habitat selection and of these habitat models, habitat types (model parameters) that did not overlap with zero were considered to significantly explain variance in hog-nosed snake occurrence.

Results

Mark-Recapture Surveys and Radio-telemetry

Of the 29 new snakes observed from 2018 to 2020, 10 were suitable candidates (4 male, 6 female) for radio transmitter implantation (Table 1.2). Of eight individuals implanted in 2018, three survived to be radio-tracked again in the following year (Table 1.2). Including the three from the previous year, a total of five individuals were tracked in 2019, with three surviving into hibernation (Table 1.3). The three individuals that survived in 2019 were tracked again in 2020 and no new suitable candidates were encountered in the 2020 field season (Table 1.2). An average number of 68.6 ± 42.2 locations/snake were recorded from the 10 implanted individuals from 2018 to 2020 (including the data collected by HSC staff in 2018). Five of the snakes were tracked for multiple years, with one individual, Snake G, radio-tracked throughout all three years (Table 1.3).

Home Ranges and Movements

From a total of 685 telemetry locations of 10 snakes over three years, mean distance moved per day (DPD; mean ± SD) was 49.0 ± 12.8 m and mean distance per move (DPM; mean ± SD) was 127.4 ± 40.7 m (Fig. 1.3). Neither DPD nor DPM were autocorrelated for any of the 10 snakes ($r < 0.6$) and snakes appeared to move to new locations approximately every two to three days. Mean distance moved per day and per move by males were greater than those of females (DPM: male = 140.1 ± 247.5 m, female = 98.3 ± 170.9 m; DPD: male = 50.5 ± 79.2 m, female = 38.2 ± 62.2 m; Fig. 1.4) but was only significantly different for distance per move (GLMM, $p < 0.05$). Although some distances per move and distances moved per day were greater in some months for males and females (Fig. 1.5 and 1.6), by month there were no significant differences between the sexes ($p > 0.05$; Table 1.3). No clear seasonal pattern in distance moved per day existed for either sex, although there were significant differences among individuals for females (n = 6) in May (GLMM, p = 0.0135), July (GLMM, p = 0.0016) and nearly so in September (GLMM, p = 0.0526), as well as for when the sexes were combined (female: n = 6, male: n = 4; July; GLMM, p = 0.0261). Like distance per day, there was also no clear seasonal pattern in distance per move among individuals for either sex, with significant differences observed when males and females were combined (female: n = 6, male: n = 4; October; GLMM, p = 0.0194) and nearly significant for females (n = 6; June and October; GLMM, p = 0.0541).

Home range sizes were calculated for eight of the 10 radio-tagged snakes (Fig. 1.7). These eight were either tracked a full active season or determined to have used their entire home range by reaching an asymptote (Fig. 1.2). Home range size (mean ± SD) for all eight snakes combined was estimated as 70.2 ± 31.9 ha based on 95% KDE (Fig. 1.8), and 63.9 ± 29.5 ha based on 95% MCP (Fig. 1.7) with 28.0 ± 25.4 ha as the core activity area (50% MCP). Although estimates of home range size using KDE were slightly larger than those based on MCP, estimates given by the two methods did not differ ($t_{(14)} = 0.41$, p = 0.69). Home range size did not significantly differ between males and females (gravid and non-gravid females combined; $t_{(3)} = -0.48$, p = 0.67) or when gravid and non-gravid females were separated (ANOVA, $F_{(1,11)} = 0.05$, p = 0.83), although male home ranges (72.01 ± 44.40 ha) were slightly larger than those of females (gravid and non-gravid combined, 59.0 ± 21.3 ha; Fig. 1.9).

General Habitat Use, Selection, and Avoidance

Beach, bluff-side, old field, and open sandy (juniper) shrubland habitats comprised the lowest amount of available habitat within the study area, while agricultural, closed-canopy forest, and human development were the three most abundant accounting for nearly 75% of available habitat (Fig. 1.1, Table 1.4). The number of snake radio-locations significantly differed among the available habitat types ($x^2 = 844.46$, df = 83, $p < 0.01$), with nearly 80% of snake locations within beach, bluff-side, forest, and riparian habitats (Table 1.4). Human development, old field, agriculture, and open sandy juniper were the least used habitat types (Table 1.4).

Snakes demonstrated non-random habitat selection. Distances from location points to available habitat types were significantly shorter than the distances from habitats to random points ($F_{(1,7)} = 217.52$, $p < 0.01$). Furthermore, the probability of snake occurrence differed among habitat types. At the landscape scale, two top models included six of eight habitats, and seven of eight habitats were most effective at predicting snake occurrence by habitat type (Table 1.5). At the home range scale, only a single top model of six habitat types significantly explained snake occurrence (Table 1.6). Of the landscape model subsets there were two top models with $\Delta AICc \leq 2$ (Table 1.5). The top model ($\Delta AICc = 0$) included all habitat types, while the other top competing model ($\Delta AICc = 1.25$) also included all habitat types, except for riparian habitat (Table 1.5). Model parameter estimates for distances to beach, forest, and old field habitats were negative, while parameter estimates for distances to bluff, crop, human, and riparian were positive at the landscape scale (Table 1.5). As such the probability of snake occurrence increased as distance from bluff, crop, human, and riparian habitats increased, but decreased as distance relative to beach, forest, and old field habitats increased. At the home range scale, forest and human habitats were highly correlated, but when run separately as univariate models, the forest model performed better as all six habitat types were significant ($p < 0.05$), compared to the significance of five out of six habitats ($p < 0.05$) in the human univariate model. Similar to the landscape scale, beach, forest, and old field had negative estimates, while bluff, crop, and riparian habitats had positive estimates at the home range scale (Table 1.6).

Discussion

Home Ranges and Movements

Sex-specific requirements likely drove the differences in movement patterns between male and female hog-nosed snakes in Huron County. Though both sexes actively seek out resources, male snakes often travel greater distances in search of mates (Gregory et al. 1987; Brito 2003). By moving frequently and extensively across the landscape to find a female, males ultimately end up travelling more than females (Gibbons and Semlitsch 1987; Gregory et al. 1987; Brito 2003). When gravid, female snakes can be less active than males (Graves and Duvall 1993; Plummer 1997; Parent and Weatherhead 2000). Decreased movement by gravid females can help fulfill the energetic demands of developing offspring (Shine 2003) and pre-oviposition ecdysis (Reinecke et al. 1980; Gaban and Farley 2002; Clayton 2012). I observed such circumstances in gravid females of the Huron County population, with decreased movement and ecdysis, even though pre-oviposition ecdysis has only been previously described in captive-bred hog-nosed snakes (Clayton 2012). Further contributing to decreased movement while gravid, females in the Huron County study population communally nested and demonstrated annual site fidelity to nesting areas, both of which have been observed in other hog-nosed snake populations (Cunnington and Cebek 2005; Buchanan 2012). When no longer gravid, females made lengthy post-oviposition movements away from the nest site. These abrupt movements post-oviposition have been observed in other populations (Robson 2011; Buchanan 2012), and for the Huron County population, females travelled to areas where they remained for the rest of the summer. However, while males most often travelled great distances, they would also remain stationary for periods at a time. It appears that Huron County eastern hog-nosed snakes demonstrate a period of decreased movement later in the active season, which has been observed in other populations where movement by eastern hog-nosed snakes decreased in the summer (Kroll 1973). As a result, it is likely that these stationary periods combined with large movements made by both sexes (females post-oviposition) contribute to the lack of significant difference in home range size between the sexes (Robson 2011; Akresh et al. 2017; Buchanan et al. 2017). Eastern hog-nosed snakes in Huron County demonstrate periods of both high activity and decreased movements, and their resulting space use has likely resulted from differences in sex-specific requirements.

In some reptile species, greater home range sizes have been recorded for populations further north in their range distribution (Weatherhead and Hoysak 1989; Carfagno and Weatherhead 2008; Martino et al. 2012). These larger home range sizes are said to result from lower productivity at higher latitudes (Brown et al. 1996; Arvisais et al. 2002; Sperry and Weatherhead 2009), that forces individuals to travel farther to acquire critical resources. Prey availability has been suggested as a driver of home range size for snake populations at northern peripheries. For example, peripheral populations of prairie rattlesnakes (*Crotalus viridis viridis*) and bullsnakes (*Pituophis catenifer sayi*) differed in space use and had larger home range sizes compared to other populations located more centrally in the range (Martino et al. 2012; Bauder et al. 2015). For eastern hog-nosed snakes in Huron County, home range size was larger than in most other conspecific populations located south of Huron County (Plummer and Mills 2000; Lagory et al. 2009; Robson 2011; Akresh et al. 2017; Buchanan et al. 2017; Vanek and Wasko 2017). As a periphery population, limited prey availability would seem like a logical explanation for the large home range size of hog-nosed snakes in Huron County. However, contradicting this hypothesis, the habitat generalist (Ontario Nature 2021) and preferred prey item of eastern hog-nosed snakes in Canada (COSEWIC 2021), the American toad (*Anaxyrus americanus*), was noticeably abundant throughout the study site (pers. obs.). Although space use by eastern hog-nosed snakes in Huron County may be partly driven by the population's northern locale, it is likely that other factors such as anthropogenic activity play a greater role. In one population of eastern hog-nosed snakes north of Huron County in Wasaga Beach, Ontario, reported home range size (183 ha) was nearly triple that of snakes in Huron County (although the method for estimating home range size in Wasaga Beach was not described; Featherstone and Anderson 2005). The large distances moved by eastern hog-nosed snakes in Wasaga Beach were attributed to avoidance of intense anthropogenic activity in the area (Featherstone and Anderson 2005; COSEWIC 2007; Cunnington pers. comm.). When the study was completed in the mid 2000s, Wasaga Beach was recognized as one of Ontario's fastest developing communities (Watters 2003) and has since seen increased anthropogenic development and human population density (Statistics Canada 2017; McSweeney 2020). Similarly, within the study area in Huron County, nearly 60% of available habitat is anthropogenically modified (Table 1.2; Figure 1.1). With greater than half of the study area human-modified in Huron County, a similar situation to the Wasaga population is likely playing out, where eastern hog-nosed snakes are moving large distances to avoid anthropogenic activity. As such, although located along the species range periphery, anthropogenic activity is likely a key influence on space use by eastern hog-nosed snakes in Huron County.

Distance moved per day (DPD) by eastern hog-nosed snakes in Huron County was significantly greater than reported in most other populations (Akresh et al. 2017; Buchanan et al. 2017; Vanek and Wasko 2017). Populations with relatively small distances moved per day and small home range sizes were located in largely natural areas with little anthropogenic development (Lagory et al. 2009; Robson 2011; Akresh et al. 2017; Buchanan et al. 2017; Vanek and Wasko 2017). The continuity of natural areas and/or presence of regular 'naturalized habitat breaks' from anthropogenic areas in these other study sites likely allowed hog-nosed snakes to carry out natural behaviours and movements (Smith et al. 2015; Lomas et al. 2019). Eastern hog-nosed snakes in Huron County, like those in Wasaga Beach (Featherstone and Anderson 2005; Cunnington pers. comm.), had to navigate a heavily modified landscape and complete relatively large movements to avoid anthropogenic activity. Animals that perceive humans as potential predators or threats are known to actively avoid anthropogenic areas, thus exhibiting home range displacement (McLellan and Shackleton 1988). Even if the anthropogenic activity or development still allows for passage (e.g., trails), movement by animals may still be restricted or altered due to immobilizing flight-or-fright responses (Andrews and Gibbons 2005; Eye et al. 2018; Lomas et al. 2019), or individuals may move uncharacteristically long-distances (Fitch and Shirer 1971; Landreth 1973; Galligan and Dunson 1979). Hog-nosed snakes in Huron County moved greater distances than snakes in most other populations, but not all (Plummer and Mills 2000; Lagory et al. 2009). An eastern hog-nosed snake population in Arkansas, had smaller home range size (50.2 ± 6.4 ha), but much higher distance moved per day (119 ± 4 m/day; Plummer and Mills 2000) compared to the Huron County population. In the Arkansas study, most of the anthropogenic activity was development that did not encourage frequent interaction with humans, making the landscape easily traversable and usable by snakes (e.g., old fields, right-of-ways, deserted fence lines; Plummer and Mills 2000). It is possible that since the Arkansas population did not frequently encounter human activity and could easily move away from the anthropogenic development, the snakes were able to move larger distances per day. However, while most of the anthropogenically modified areas in Arkansas were still vegetated, they may have lacked suitable refuge sites. It has been suggested that snakes will generally avoid open areas (Shine et al. 2004; Clark et al. 2010; Ettling et al. 2013) due to lack of cover within anthropogenically-modified landscapes (Eye et al. 2018). As such, while hog-nosed snakes largely avoided human-modified areas in Huron County, there may have been enough natural habitats with suitable refugia available for snakes to minimize daily movements relative to those in the Arkansas population. It appears that remnant natural areas play a critical role in hog-nosed snake space use. Further loss of natural areas from Huron County would likely impact space use by snakes, causing distances moved to increase, thus increasing chances of negative interactions with humans.

General Habitat Use, Selection, and Avoidance

Habitats dominated by woody vegetation influenced occurrence of Huron County hog-nosed snakes. For example, upland forest was positively associated with eastern hog-nosed snake occurrence, while bluff-side was negatively associated with snake occurrence. While I did not distinguish forest types in the modelling, few snake locations were within conifer-dominant stands. Thermoregulation is a key driver in habitat selection by snakes (Huey et al. 1989; Reinert 1993; Blouin-Demers and Weatherhead 2001) and factors such as breaks in the overhead canopy (Canham et al. 1990; Robson 2011; Akresh et al. 2017), open habitat patches (Kjoss and Litvaitis 2001), and forest edges (Blouin-Demers and Weatherhead 2001; Carfagno and Weatherhead 2006; DeGregorio et al. 2015) allow snakes to associate with wooded areas. For eastern hog-nosed snakes, suitable thermal habitat is also associated with gaps in the overhead canopy (Robson 2011; Akresh et al. 2017) and has allowed the species to associate with forested areas (Lagory et al. 2009; Thomasson and Blouin-Demers 2015; Vanek and Wasko 2017). In southern Ontario, deciduous ash trees (*Fraxinus* sp.) have been decimated by infestations of the invasive emerald ash borer (*Agrilus planipennis*; OMNRF 2020; Zong et al. 2020) and ash trees in Huron

County also are largely infected. In addition to naturally aged trees, trees downed by ash borer infestation have created numerous large gaps in the forest canopy, thereby creating more suitable thermoregulatory habitat for snakes. With these factors creating an abundance of suitable thermal habitat, eastern hog-nosed snakes can frequently use and positively associate with upland forest habitat in Huron County. Although bluff-side habitat has areas that remain forested, the bluff is largely unstable, as erosion has created unpredictable habitat. Thus, hog-nosed snakes still use bluff habitat, but use it temporarily as a corridor to travel between beach and upland areas during the active season, as well as for overwintering by some individuals.

While the relatively low overstory and sandy substrates of *Juniperus* shrubland would suggest it is likely important to eastern hog-nosed snakes, I found that it was not a significant habitat for snakes in Huron County. At 0.8%, *Juniperus* shrubland was one of the least available habitat types, had less than 4% of telemetry locations, and was the only habitat not included in the modelling (unacceptably high correlation > 0.6 with beach habitat). In other snake species that use shrub-dominated habitats, size and availability of shrub habitats are known to influence occupancy. The North American racer (*Coluber constrictor*) is a relatively mobile species that prefers shrubland or early-successional habitats (Kjoss and Litvaitis 2001; Martino et al. 2012), and in one particular study, racers were found to avoid using small to intermediate-sized early-succession habitat patches (Kjoss and Litvaitis 2001). This avoidance, in combination with greater habitat fragmentation, was thereby suggested as a prominent factor contributing to the species regional decline across the northeastern United States (Kjoss and Litvaitis 2001). Because eastern hog-nosed snakes are also highly mobile and known to use shrub-dominated habitat (COSEWIC 2007; Seburn 2009), with so little *Juniperus* shrubland available in Huron County, it appears that snakes opt to use other open canopied and/or sand-based habitats instead.

Beaches and dune habitat are critical to some snake species. For example, in one population of bullsnakes (*Pituophis catenifer sayi*), beach was the habitat most frequently used, with actual use 92 times greater than expected use (Edkins 2017). In a population of South American hog-nosed snakes (*Xenodon dorbignyi*) along the northern coast of Brazil, dune habitat was preferred (Tozetti et al. 2009; Tozetti et al. 2010). Eastern hog-nosed snakes are also often associated with dune habitat (Michener and Lazell 1989; Cunnington and Cebek 2005; Buchanan et al. 2017). Populations in Canada have demonstrated disproportionately high use of beach dunes along the Great Lakes shoreline (Featherstone and Anderson 2005; Robson 2011) and use this habitat for nesting (Cunnington and Cebek 2005; Robson 2011), foraging for preferred prey item, Fowler's toad (*Anaxyrus fowleri*) which also require sandy soils (Gillingwater and Piraino 2004; COSEWIC 2007; COSEWIC 2010), and like other fossorial snakes, for refuge to escape ground surface conditions (Oliveira et al. 2001; Tozetti et al. 2009). Huron County hog-nosed snake occurrence was positively associated with beach habitat and like other conspecific populations, beach habitat was used for nesting, foraging, and refuge, and had a disproportionately large number of telemetry locations. While females laid eggs in dune habitat, both sexes used the beach for overwintering (Gallon et al. 2021); one burrow was used for solitary overwintering by different individuals across years (e.g., Snake F used in 2018, then Snake J used for 2019 and 2020; Gallon et al. 2021). Huron County snakes also used beach habitat for short-term refuge and rather than burrowing in the sand, individuals hid amongst driftwood along the shoreline. Use of driftwood by snakes in coastal areas is not uncommon. Dekay's brownsnakes (*Storeria dekayi*) in Long Point, Ontario were regularly observed using washed up driftwood on beach dunes for predator protection and suitable microclimatic conditions (Hecnar and Hecnar 2011). Although eastern hog-nosed snakes have the ability to burrow in sand, using driftwood in ways similar to *Storeria dekayi* is likely a less energetically-taxing behaviour. Although availability of beach habitat was low compared to other habitats, its various resources and ways in which snakes can use them, make beaches valuable to eastern hog-nosed snakes in Huron County.

Reptiles in general do not show a universal preference or avoidance for anthropogenically-modified areas. For example, even if natural refugia are readily available, some species prefer to use human modified areas (Koenig et al. 2001; Kwiatkowski et al. 2008; Edkins 2017). For others, anthropogenic activity and infrastructure have led to local population declines (Row et al. 2007). Twenty-eight percent of available habitat (not including agricultural land), the highest proportion, in Huron County was anthropogenically developed and eastern hog-nosed snakes largely avoided these areas. At the landscape scale, anthropogenically-developed habitat was negatively associated with eastern hog-nosed snake occurrence and constituted less than 8% of telemetry locations. In contrast, the opposite trend was reported in two other Ontario populations. In the Georgian Bay region, areas with human development were preferred by eastern hog-nosed snakes over rock-barren or wetland habitats (Rouse 2006), while for the Long Point region, developed areas were the second most preferred habitat (Robson 2011). In these other areas, anthropogenically-developed habitat was minute compared to other available habitat types (Rouse 2006; Robson 2011), so the risks associated with this habitat were likely not as severe as in the heavily modified landscape of Huron County. While large portions of the landscape have been converted to residential infrastructure, cottages, roads, and hiking trails, these were not the only anthropogenic developments in the Huron County area. Infrastructure associated with a local airport and marina were also present, and negatively influenced eastern hog-nosed snakes. Although the airport runway is relatively permeable, no telemetered snakes were observed directly crossing the airstrip; however, snakes were located within habitats surrounding the airstrip. Not all eastern hog-nosed snakes successfully avoided the detrimental impacts of aviation activity. In 2014, prior to in-depth monitoring by the Huron Stewardship Council, an eastern hog-nosed snake resting in a fissure in the runway was killed by a runway sweeper (Huron Stewardship Council, unpublished data). Aviation infrastructure has been reported near one other eastern hog-nosed snake population at Cape Cod National Seashore, USA, where no instances of aviation-induced mortality were reported (Buchanan 2012). It appears that since the Cape Cod study site was nearly 12x larger than the Huron County site, the runway in Huron County comprised proportionally less area overall so eastern hog-nosed snakes were able to avoid aviation activity, as indicated by a lack of home range overlap with airport infrastructure (Buchanan 2012). With a much smaller but more impacted area overall, it appears that eastern hog-nosed snakes in Huron County cannot avoid human activity, and this has implications for their survival.

Agricultural land was also not frequented by eastern hog-nosed snakes in Huron County. Some reptile species are known to prefer natural areas and avoid cropland altogether (Durner and Gates 1993; Ettling et al. 2013). While density of cropland reduces availability of suitable habitat for eastern hog-nosed snakes (Thomasson and Blouin-Demers 2015) in Huron County, use by hog-nosed snakes appeared to depend on whether lands were actively cultivated or fallow, and the type of crop planted in the actively cultivated land. Snakes were positively associated with fields that were once cultivated but sat fallow or had been reclaimed into meadow habitat. There are mixed observations regarding eastern hog-nosed snakes using old field habitat. While old fields were frequently used by some populations (Rouse 2006; Lagory et al. 2009), they were actively avoided by others (Cunnington 2004). In Huron County, old fields were positively associated with snake occurrence, while actively cultivated fields were largely avoided by eastern hog-nosed snakes. In 2018, no radio-tracked snakes used the fields when they were seeded with soybeans, but in 2019 when the fields were seeded with wheat, three tracked snakes used the fields multiple times. Although active fields may have been used by some snakes, cropland use presented threats. A snake that had previously used the fields in 2019 was killed by farm equipment reseeding the fields in late May 2020. While cropland was seeded again with soy in 2020, I was not able to directly quantify if type of crop cover influenced eastern hog-nosed snake use. As such, like many species in Canada, it appears that eastern hog-nosed snakes in Huron County are endangered in part by agricultural activity (COSEWIC 2002; Kerr and Cihlar 2004; Environment Canada 2016).

Habitat modelling indicated that hog-nosed snakes in Huron County generally did not prefer riparian areas although nearly 17% of telemetry locations occurred in riparian habitat. While hog-nosed snakes in other populations generally do not use riparian habitat (Lagory et al. 2009; Robson 2011; Vanek and Wasko 2017), snakes in Huron County are not the first to use riparian areas. Hog-nosed snakes in Wasaga Beach, Ontario used large river riparian habitat and even crossed the large river system (Featherstone and Anderson 2005). Similarly, some females in Huron County spent large portions of the active season within riparian floodplain, and post oviposition, some females crossed the watercourse and occupied islands in the middle of the river. In both cases, the females remained in these areas until it was time to move back to their overwintering sites. The resources offered by riparian areas can be beneficial to snakes, even if they are not fully or semi-aquatic species. Some examples of other snake species that have been associated with riparian habitat include the eastern foxsnake (*Pantherophis vulpinus gloydi*) (COSEWIC 2008; Row et al. 2012), eastern massasauga rattlesnake (*Sistrurus catenatus*;

Weatherhead and Prior 1992; COSEWIC 2012), and the eastern yellow-bellied racer (*Coluber constrictor flaviventris*; Martino et al. 2012). However, use of riparian areas may not always be year-round. Eastern yellow-bellied racers are known to travel between upland and lowland areas (Martino et al. 2012), and like other reptiles in temperate zones using upland habitat for hibernation, then travelling to low-land riparian areas during the summer (Semlitsch and Bodie 2003; Martino et al. 2012). Therefore, as a temperate reptile residing in a landscape with limited natural areas, it appears that resources within riparian zones are also beneficial to eastern hog-nosed snakes in Huron County.

Conclusions

The highly modified landscape of Huron County challenges snake space use. While pockets of natural habitat exist, anthropogenic activity is extensive, impacting the spatial ecology and habitat use of relatively mobile species like the eastern hog-nosed snake. While natural habitats like forest, beach, and old field were used and preferred by eastern hog-nosed snakes, widespread human-modified areas appear to have caused eastern hog-nosed snakes to adjust their space and habitat use. As such, to navigate widespread human activity and reach natural habitats, Huron County eastern hog-nosed snakes moved greater distances per day and had larger home range sizes compared to snakes in most other conspecific populations. Although patches and small areas of contiguous natural habitat are available, eastern hog-nosed snakes could not always avoid areas of human activity and were exposed to fatal agricultural and aviation activities. Although populations in other locations face similar pressures, a diversity of land uses across Huron County present unique threats for this population of eastern hog-nosed snakes.

To ensure the persistence of eastern hog-nosed snakes in Huron County, threats from anthropogenic land use should be carefully considered when designing and implementing recovery and management strategies. I would suggest these strategies should include continuing community outreach and habitat enhancement, as well as continuing to work closely with local stakeholders, including airport staff, marina owners, and other landowners. Maintaining relations and a presence amongst members of the community encouraged individuals to report snake sightings. This in turn served and will continue to serve as a valuable tool in passively monitoring snake locations and will continue to help fill knowledge gaps about population persistence and distribution of hog-nosed snakes within Huron County. Current understanding of eastern hog-nosed snake distribution in Huron County demonstrates the arbitrary nature of anthropogenically established boundaries. While hog-nosed snakes frequented natural habitats, they have also been found amongst residential garden beds, agricultural fields, airport infrastructure, and have critical nesting and overwintering habitat within proximity of the marina. As such, it will be crucial to continue to work closely with stakeholders in the area not only for land access to survey for snakes but also to preserve important areas with hog-nosed snake habitat, as well as to generate support when pursuing habitat enhancement projects. As a mobile species, enhancing habitat connectivity would play a critical role in ensuring population persistence in Huron County. To do so would optimally entail enhancement or restoration of human-modified areas, that otherwise act as bottlenecks for eastern hog-nosed snakes. For agricultural fields, one option may include seeding cover crops during periods of rest if fields are otherwise seeded with cash crops. Reptiles that use cropland are often injured (Saumure and Bider 1998; Wallace 2020) or killed (Durbian 2006; Deák et al. 2020) by agricultural machinery, so restoring the fields back to meadow vegetation would be most beneficial as permanent snake habitat, in addition to being ideal for the airport (to preserve an open field of view surrounding the runway). Through community involvement and education, preservation of critical hog-nosed snake habitat, and pursuing avenues of habitat enhancement, the population of eastern hog-nosed snakes in Huron County will more likely persist for years to come, so that others can enjoy these incredible, charismatic snakes.

Literature Cited

Aebischer, N.J., Robertson, P.A., and Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology **74**: 1313-1325.

Akresh, M.E., King, D.I., Timm, B.C., and Brooks, R.T. 2017. Fuels management and habitat restoration activities benefit eastern hognose snakes (*Heterodon platirhinos*) in a disturbance-dependent ecosystem. Journal of Herpetology **51**(4): 468-476.

Andrews, K.M., and Gibbons, J.W. 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. Copeia **2005**: 772-782.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management **74**: 1175-1178.

Arvisais, M., Bourgeois, J.C., Lévesque, E., Daigle, C., Masse, D., and Jutras, J. 2002. Home range and movements of a wood turtle (*Clemmys insculpta*) population at the northern limit of its range. Canadian Journal of Zoology **80**: 402-408.

Barton, K. 2019. MuMIn: Multi-model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn.

Bates, D., Machler, M., Bolker, B.M., and Walker, S.C. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**: 1-48.

Bauder, J.M. Akenson, H., and Peterson, C.R. 2015. Movement patterns of prairie rattlesnakes (*Crotalus v. viridis*) across a mountainous landscape in a designated wilderness area. Journal of Herpetology **49**(3): 377-387.

Beale, M., Poulin, S., Ivanyi, C., and Blouin-Demers, G. 2016. Anthropogenic disturbance affects movement and increases concealment in western diamondback rattlesnakes (*Crotalus atrox*). Journal of Herpetology **50**(2): 216-221.

Bishir, S.C., Hossack, B.R., Fishback, L., and Davenport, J.M. 2018. Post-breeding movement and habitat use by wood frogs along an Arctic-Subarctic ecotone. Arctic, Antarctic, and Alpine Research **50**(1): 1-9.

Blouin-Demers, G., and Weatherhead, P.J. 2001. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes *Elaphe obsoleta obsoleta*. Journal of Animal Ecology **70**: 1006-1013.

Bohm, M., Collen, B., Baillie, J.E.M., Bowler, P., Chanson, J., Cox, N., …, and, Zug, G. 2013. The conservation status of the world's reptiles. Biological Conservation **157**: 372-385.

Boyle, S.A., Lourenço, W.C., Da Silva, L.R., and Smith, A.T. 2009. Home range estimates vary with sample size and methods. Folia Primatologica **80**(1): 33-42.

Brito, J.C. 2003. Seasonal variation in movements, home range, and habitat use by male *Vipera latastei* in northern Portugal. Journal of Herpetology **37**: 155-160.

Brown, J.H., Stevens, G.C., and Kaufman, D.M. 1996. The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecological Systematics **27**: 597-623.

Buchanan, S.W. 2012. Ecology of the eastern hognose snake (*Heterodon platirhinos*) at Cape Cod National Seashore, Barnstable County, Massachusetts. M.Sc. Thesis, Biology, Montclair State University, Montclair, New Jersey.

Buchanan, S.W., Timm, B.C., Cook, R.P., Couse, R., and Hazard, L.C. 2017. Spatial ecology and habitat selection of eastern hognose snakes. Journal of Wildlife Management **81**(3): 509-520.

Burgman, M.A. and Fox, J.C. 2003. Bias in species range estimates from minimum convex polygons: Implications for conservation and options for improved planning. Animal Conservation **6**(1): 19-28.
Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd Edition, Springer-Verlag, New York, NY, USA.
Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling **197**(3-4): 516-519.
Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Pries, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research **20**(5): 620-631.
Carfagno, G.L.F. and Weatherhead, P.J. 2006. Intraspecific and interspecific variation in use of forest-edge habitat by snakes. Canadian Journal of Zoology **84**: 1440-1452.
Carfagno, G.L.F. and Weatherhead, P.J. 2008. Energetics and space use: intraspecific and interspecific comparisons of movements and home ranges of two Colubrid snakes. Journal of Animal Ecology **77**: 416-424.
Casper, G.S., Anton, T.G., Hay, R.W., Holycross, A.T., King, R.S., Kingsbury, B.A., Mauger, D., Parent, C., Phillips, C.A., Resetar, A., Seigel, R.A., and Wilson, T.P. 2001. Recommended standard survey protocal for the Eastern Massasauga, *Sisturus catenatus catenatus*. US Fish and Wildlife Service, Fort Snelling, MN. 9 pp.
CNES (Centre National d’Etudes Spatiales). 2020. Aerial Imagery. Centre National d’Etudes Spatiales, Paris, France.
Clark, R.W., Brown, W.S., Stechert, R., and Zamudio, K.R. 2010. Roads, interrupted dispersal, and genetic diversity in Timber Rattlesnakes. Conservation Biology **24**: 1059-1069.
Clayton, J. 2012. Care and Breeding the Western Hog-nosed Snake. Available from: https://www.reptilesmagazine.com/care-and-breeding-the-western-hog-nosed-snake/ [Accessed 02 January 2021].
Conant, R., and Collins, J.T. 1998. A Field Guide to Reptiles and Amphibians: Eastern and Central North America. Houghton Mifflin Co. New York, NY, USA.
Corey, B., and Doody, J.S. 2010. Anthropogenic influences on the spatial ecology of a semi-arid python. Journal of Zoology **281**: 293-302.
COSEWIC. 2002. COSEWIC Assessment and Status Report on the Gophersnake *Pituophis catenifer* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 33 pp.
COSEWIC. 2007. COSEWIC Assessment and Update Status Report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. viii + 36 pp.
COSEWIC. 2008. COSEWIC Assessment and Update Status Report on the Eastern Foxsnake *Elaphe gloydi*, Carolinian and Great Lakes/St. Lawrence population, in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 45 pp.
COSEWIC. 2010. COSEWIC Assessment and Status Report on the Fowler’s Toad *Anaxyrus fowleri* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa vii + 58 pp.
COSEWIC. 2012. COSEWIC Assessment and Status Report on the Massasauga *Sistrurus catenatus* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xiii + 84 pp.

COSEWIC. 2021. COSEWIC Assessment and Update Status Report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xi + 45 pp.

Crawshaw, G., and Lentini, A. 2013. Invasive Procedures Protocol for Snakes. Prepared for the Animal Care Committee.

Cummings, F.H., Morris, K., and McLennan, D. 1998. Economic Impact of Agriculture on the Economy of Huron County. School of Rural Planning and Development. University of Guelph, Guelph, ON. pp. 1-58.

Cunnington, G. 2004. Modelling habitat use by eastern hog-nosed snakes (*Heterodon platirhinos*) in Wasaga Beach Provincial Park, Ontario. Undergraduate thesis, Trent University, Peterborough, Ontario.

Cunnington, G.M. and Cebek, J.E. 2005. Mating and nesting behavior of the eastern hognose snake (*Heterodon platirhinos*) in the northern portion of its range. American Midland Naturalist **154**(2): 474-478.

Deák, G., Katona, K., and Biró, Z. 2020. Exploring the use of a carcass detection dog to assess mowing mortality in Hungary. Journal of Vertebrate Biology **69**(3): 1-9.

DeGregorio, B.A., Westervelt, J.D., Weatherhead, P.J., and Sperry, J.H. 2015. Indirect effect of climate change: shifts in ratsnake behavior alter intensity and timing of avian nest predation. Ecological Modelling **312**: 239-245.

Duhatschek, P. 2018. The Huron County snake that pretends to be something it's not. Available from: https://www.cbc.ca/news/canada/london/eastern-hognosed-snake-huron-county-1.4644127 [Accessed 8 October 2019].

Durbian, F.E. 2006. Effects of mowing and summer burning on the massasauga (*Sistrurus catenus*). American Midland Naturalist **155**: 329-334.

Durner, G.M., and Gates, J.E. 1993. Spatial ecology of black rat snakes on Remington Farms, Maryland. Journal of Wildlife Management **57**(4): 812-826.

Eastern Massasauga Recovery Team (EMRT). 2005. Guidelines for identifying significant habitat, and significant wildlife habitat, for the Massasauga in Eastern Georgian Bay and Bruce Peninsula Populations, Ontario. Version 1.0.

Edge, C.B., Steinberg, B.D., Brooks, R.J., and Litzgus, J.L. 2010. Habitat selection by Blanding's turtles (*Emydoidea blandingii*) in a relatively pristine landscape. Ecoscience **17**: 90-99.

Edkins, T.L. 2017. Variable habitat selection and space use among bullsnake (*Pituophis catenifer sayi*) populations: distance between seasonal habitats drives space use. M.Sc. Thesis, Biology, University of Regina, Regina, Saskatchewan.

Environment Canada. 2016. Recovery Strategy for the Wood Turtle (*Glyptemys insculpta*) in Canada [Proposed]. *Species at Risk Act* Recovery Strategy Series. Environment Canada, Ottawa. v + 48 pp.

Ernst, C.H., and Ernst, E.M. 2003. Snakes of the United States and Canada. Smithsonian Books, Washington, DC, USA.

ESRI. 2021. ArcMap 10.5.1. Environmental Systems Research Institute, Redlands, California.

Ettling, J.A., Aghasyan, L.A., Aghasyan, A.L., and Parker, P.G. 2013. Spatial ecology of Armenian vipers, *Montivipera raddei*, in a human-modified landscape. Copeia **2013**: 64-71.

Ettling, J.A., Aghasyan, L.A., Aghasyan, A.L., and Parker, P.G. 2016. Spatial ecology of Armenian vipers, *Montivipera raddei*, in two different landscapes: human-modified vs. recovered natural. Russian Journal of Herpetology **23**(2): 93-102.

Eye, D.M., Maida, J.R., McKibbin, O.M., Larsen, K.W., and Bishop, C.A. 2018. Snake mortality and cover board effectiveness along exclusion fencing in British Columbia, Canada. Canadian Field Naturalist **132**: 30-35.

Featherstone, D. and Anderson, S. 2005. Eastern Hog-nosed Snake Discussion Paper. Prepared for Nottawasaga Valley Conservation Authority, Wasaga Beach, ON. viii + 24 pp.

Fitch, H.S. 1993. Relative abundance of snakes in Kansas. Transaction of the Kansas Academy of Science **1903**: 213-224.

Fitch, H.S., and Shirer, H.S. 1971. A radiotelemetric study of spatial relationships in some common snakes. Copeia **1971**: 118-128.

Ford, N.B., Cobb, V.A., and Stout, J. 1991. Species diversity and seasonal abundance of snakes in a mixed pine-hardwood forest of eastern Texas. Southwestern Naturalist **36**: 171-177.

Gaban, R.D. and Farley, R.D. 2002. Ecdysis in scorpions: supine behavior and exuvial ultrastructure. Invertebrate Biology **121**(2): 136-147.

Galligan, J.H. and Dunson, W.R. 1979. Biology and status of timber rattlesnake (*Crotalus horridus*) populations in Pennsylvania. Biological Conservation **15**: 13-58.

Gallon, A., Maddalena, M. and Watt, C. 2021. Eastern Hog-nosed Snake Conservation in Huron County: Final 2020/2021 Report. Unpublished report to Ontario Ministry of Natural Resources and Forestry. Huron Stewardship Council. Huron County, ON. i + 32 pp.

Gibbons, J.W., and Semlitsch, R.D. 1987. Activity patterns. *In*: Snakes: Ecology and Evolutionary Biology, Seigel, R.A., Collins, J.T., Novak, S.S. (eds.). Collier Macmillan, Toronto, ON, pp: 396-421.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., and Winne, C.T. 2000. The global decline of reptiles, déjà vu amphibians. BioScience **50**(8): 653-666.

Gillingwater, S.D., and Piraino, T.J. 2004. Chelonian survey and research study of the Big Creek National Wildlife Area (2003) and selective herpetofaunal survey, inventory and research study of the Long Point National Wildlife Area (1996-1999, 2003). Unpublished report to Big Creek National Wildlife Area, 65 pp + appendix.

Graves, B.M. and Duvall, D. 1993. Reproduction, rookery use, and thermoregulation in free-ranging, pregnant *Crotalus v. viridis*. Journal of Herpetology **27**: 33-41.

Gregory, P.T., Macartney, J.M., and Larsen, K.W. 1987. Spatial patterns and movements. *In*: Snakes: Ecology and Evolutionary Biology, Seigel, R.A., Collins, J.T., Novak, S.S. (eds.). Collier Macmillan, Toronto, ON, pp: 366-395.

Griffiths, R.A., Foster, J., Wilkinson, J.W., and Sewell, D. 2015. Science, statistics and surveys: a herpetological perspective. Journal of Applied Ecology **52**: 1413-1417.

Halliday, W., and Blouin-Demers, G. 2015. Efficacy of coverboards for sampling small northern snakes. Herpetology Notes **8**: 309-314.

Harding, J.H. 1997. Amphibians and Reptiles of the Great Lakes Region. University of Michigan Press, Ann Arbor, MI. 378 pp.

Harvey, D.S. 2008. Massasauga monitoring—analysis and recommendations v.1.2. Report submitted to the Bruce Peninsula National Park / Fathom Five National Marine Park, Parks Canada Agency, Ontario.

Hansteen, T.L., Andreassen, H.P., and Ims, R.A. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. Journal of Wildlife Management **61**: 280-290.
Hecnar, S.J. and Hecnar, D.R. 2011. Microhabitat selection of woody debris by Dekay's brownsnake (*Storeria dekayi*) in a dune habitat in Ontario, Canada. Journal of Herpetology **45**(4): 478-483.
Hoffman, D.W., Richards, N.R., and Morwick, F.F. 1952. Soil Survey of Huron County. Ontario Soil Survey Rep. No. 13, Experimental Farms Service, Canada Department of Agriculture, and Ontario Agricultural College, Guelph, ON.
Howze, J.M., Sash, K.J., Carroll, J.P., and Smith, L.L. 2019. A regional scale assessment of habitat selection and home range of the eastern rat snake in pine-dominated forests. Forest Ecology and Management **432**: 225-230.
Huey, R.B., Peterson, C.R., Arnold, S.J. and Porter, W. 1989. Hot rocks and not-so-hot rocks: retreat site selection by garter snake and its thermal consequences. Ecology **70**: 931-934.
Huron County. 2015. South Western Ontario Orthoimagery Project (SWOOP) Aerial Imagery. Huron County, Ontario.
Hurvich, C.M., and Tsai, C. 1989. Regression and time series model selection in small samples. Biometrika **76**(2): 297-307.
Jenkins, C.L., Peterson, C.R., Doering, S.C., and Cobb, V.A. 2009. Microgeographic characteristics among Western Rattlesnake (*Crotalus oreganus*) populations. Copeia **2009**: 774-780.
Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology **61**(1): 65-71.
Kerr, G.D., Bull, C.M., and Mackay, D. 2004. Human disturbance and stride frequency in the sleepy lizard (*Tiliqua rugosa*): implications for behavioral studies. Journal of Herpetology **38**(4): 519-526.
Kerr, J.T. and Cihlar, J. 2004. Patterns and causes of species endangerment in Canada. Ecological Applications **14**: 743-753.
Kjoss, V.A., and Litvaitis, J.A. 2001. Community structure of snakes in a human-dominated landscape. Biological Conservation **98**(3): 285-292.
Koenig, J., Shine, R., and Shea, G. 2001. The ecology of an Australian reptile icon: how do blue-tongue lizards (*Tiliqua scincoides*) survive in suburbia? Wildlife Research **28**: 215-227.
Kraus, T. 2011. Recovery Strategy for the Eastern Hog-nosed Snake (*Heterodon platirhinos*) in Ontario. Ontario Recovery Strategy Series. Prepared for the Ontario Ministry of Natural Resources, Peterborough, Ontario. i + 6 pp. + Appendix vi + 24 pp. Adoption of the Recovery Strategy for the Eastern Hog-nosed Snake (*Heterodon platirhinos*) in Canada (Seburn, 2009).
Kroll, J.C. 1973. Comparative physiological ecology of eastern and western hognose snakes (*Heterodon platirhinos* and *Heterodon nasicus*). PhD. thesis, Texas A&M University, College Station, Texas. 261 pp.
Kwiatkowski, M.A., Schuett, G.W., Repp, R.A., Nowak, E.M., and Sullivan, B.K. 2008. Does urbanization influence the spatial ecology of Gila monsters in the Sonoran Desert? Journal of Zoology **276**: 350-357.
Lagory, K.E., Walston, L.J., Goulet, C., Van Lonkhuyzen, R.A., Najjar, S., and Andrews, C. 2009. An examination of scale-dependent resource use by eastern hognose snakes in Southcentral New Hampshire. Journal of Wildlife Management **78**(3): 1387-1393.

Landreth, H.F. 1973. Orientation and behavior of the rattlesnake, *Crotalus atrox*. Copeia **1973**: 26-31.

Langen, T.A., Machniak, A., Crowe, E.K., Mangan, C., Marker, D.F., Liddle, N., and Roden, B. 2007. Methodologies for surveying herpetofauna mortality on rural highways. Journal of Wildlife Management **71**(4): 1361-1368.

Laverty, J.F., Korol, B., and Litzgus, J.D. 2016. Measuring the effects of water-based recreation on the spatial ecology of eastern musk turtles (*Sternotherus odoratus*) in a provincial park in Ontario, Canada. Copeia **104**(2): 440-447.

Lesbarrères, D., Ashpole, S.L., Bishop, C.A., Blouin-Demers, G., Brooks, R.J., Echaubard, P., Govindarajulu, P., Green, D.M., Hecnar, S.J., Herman, T., Houlahan, J., Litzgus, J.D., Mazerolle, M.J., Paszkowski, C.A., Rutherford, P., Schock, D.M., Storey, K.B., and Lougheed, S.C. 2014. Conservation of herpetofauna in northern landscapes: threats and challenges from a Canadian perspective. Biological Conservation **170**: 48-55.

Leuenberger, W. Davis, A.G., McKenzie, J.M., Drayer, A.N., and Price, S.J. 2019. Snake density using passive integrated transponder (PIT) telemetry and spatial capture-recapture analyses for linear habitats. Journal of Herpetology **4**: 272-281.

Lomas, E., Maida, J., Bishop, C.A., and Larsen, K.W. 2019. Movement ecology of northern pacific rattlesnakes (*Crotalus o. oreganus*) in response to disturbance. Herpetologica **75**(2): 153-161.

Maddalena, M. 2019. Eastern Hog-nosed Snake Conservation in Huron County: Final 2018/2019 Report. Unpublished report to Ontario Ministry of Natural Resources and Forestry. Huron Stewardship Council. Huron County, ON. i + 20 pp.

Manly, B.F. J., McDonald, L.L., Thomas, D.L., McDonald, T.L., and Erickson, W.P. 2002. Resource selection by animals: statistical design and analysis of field studies. Kluwar Academic Publishers, Dordrecht, The Netherlands. pp. 29.

Martino, J.A., Poulin, R.G., Parker, D.L., and Somers, C.M. 2012. Habitat selection by grassland snakes at northern range limits: implications for conservation. Journal of Wildlife Management **76**(4): 759-767.

McSweeney and Associates. 2020. Socio-Economic Profile for the Town of Wasaga Beach. Report to the Town of Wasaga Beach. vi + 42 pp.

McLellan, B.N., and Shackleton, D.M. 1988. Grizzly bears and resource extraction industries: effects of roads on behaviour, habitat use and demography. Journal of Applied Ecology **25**: 451-460.

Michener, M.C., and Lazell, J.D. 1989. Distribution and relative abundance of the hognose snake, *Heterodon platirhinos*, in eastern New-England. Journal of Herpetology **23**: 35-40.

Millar, C.S., and Blouin-Demers, G. 2011. Spatial ecology and seasonal activity of blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada. Journal of Herpetology **45**(3): 370-378.

Moore, J.A., and Gillingham, J.C. 2006. Spatial ecology and multi-scale habitat selection by a threatened rattlesnake: The eastern massasauga (*Sistrurus catenatus catenatus*). Copeia **2006**(4): 742-751.

Moore, M.J.C., and Seigel, R.A. 2006. No place to nest or bask: Effects of human disturbance on the nesting and basking habits of yellow-blotched map turtles (*Graptemys flavimaculata*). Biological Conservation **130**: 386-393.

Neyman, J. 1934. On the two different aspects of the representative method: the method of stratified sampling and the method of purposive selection. Journal of the Royal Statistical Society **97**: 558-625.

Nilsen, E.B., Pedersen, S., and Linnell, J.D.C. 2008. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecological Research **23**: 635-639.

Oliveira, R.B., Di-Bernardo, M., Pontes, G.M.F., Maciel, A.P. and Krause, L. 2001. Dieta e comportamento alimentar da cobra nariguda, *Lystrophis dorbignyi* (Duméril, Bibron & Duméril, 1854) no Litoral Norte do Rio Grande do Sul, Brasil. Cuadernos de Herpeolgía **14**(2): 117-122.

OMNRF. 2016a. Eastern Hog-nosed Snake Government Response Statement. Ontario Ministry of Natural Resources and Forestry, Species Conservation Policy Branch. Peterborough, ON. 6 pp.

OMNRF. 2016b. Survey Protocol for Ontario's Species at Risk Snakes. Ontario Ministry of Natural Resources and Forestry, Species Conservation Policy Branch. Peterborough, ON. ii + 17 pp.

OMNRF. 2018. The Ecosystems of Ontario—Part 1: Ecozones and Ecoregions. Available from: https://www.ontario.ca/page/ecosystems-ontario-part-1-ecozones-and-ecoregions [Accessed 27 November 2019].

OMNRF. 2019. Species at risk: eastern hog-nosed snake. Available from: https://www.ontario.ca/page/eastern-hog-nosed-snake [Accessed 02 March 2021].

OMNRF. 2020. Emerald ash borer. Available from: https://www.ontario.ca/page/emerald-ash-borer [Accessed 06 February 2021].

Ontario Nature. 2021. American Toad. Available from: https://ontarionature.org/programs/citizen-science/reptile-amphibian-atlas/american-toad/ [Accessed 31 May 2021].

Parent, C., and Weatherhead, P. J. 2000. Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. Oecologia **125**(2): 170-178.

Parker, W.S., and Plummer, M.V. 1987. Population ecology. *In* Snakes: Ecology and Evolutionary Biology. *Edited by*: Seigel, R.A., Collins, J.T., Novak, S.S. McGraw-Hill, New York. pp. 253-301.

Peet-Paré, C.A., and Blouin-Demers, G. 2012. Female eastern hog-nosed snakes (*Heterodon platirhinos*) choose nest sites that produce offspring with phenotypes likely to improve fitness. Canadian Journal of Zoology **90**: 1215-1230.

Plummer, M.V. 1997. Speed and endurance of gravid and nongravid green snakes *Opheodrys aestivus*. Copeia **1994**: 191-194.

Plummer, M.V. and Mills, N.E. 2000. Spatial ecology and survivorship of resident and translocated hognose snakes (*Heterodon platirhinos*). Journal of Herpetology **34**(4): 565-575.

Reinecke, J.P, Buckner, J.S. and Grugel, S.R. 1980. Life cycle of laboratory-reared tobacco hornworms *Manduca sexta*, a study of development and behavior, using time-lapse cinematography. The Biological Bulletin **158**(1): 129-140.

Reinert, H.K. 1993. Habitat selection in snakes. *In* Snakes: Ecology and Evolutionary Biology *Edited by*: Seigel, R.A., Collins, J.T., and Novak, S.S. McGraw-Hill, New York. pp. 201-240.

Robson, L.E. 2011. The spatial ecology of eastern hognose snakes *(Heterodon platirhinos*): habitat selection, home range size, and the effect of roads on movement patterns. M.Sc. thesis, Biology, University of Ottawa, Ottawa, Ontario.

Rouse, J. 2006. Spatial ecology of the eastern massasauga (*Sisturus catenatus*) and the eastern hog-nosed snake (*Heterodon platirhinos*) in a rock-barren landscape. M.Sc. thesis. University of Guelph, Guelph, Ontario.

Rouse, J.D., Wilson, R.J., Black, R., and Brooks, R.J. 2011. Movement and spatial dispersion of *Sisturus catenatus* and *Heterodon platirhinos*: Implications for interactions with roads. Copeia **2011**(3): 443-456.

Row, J.R. and Blouin-Demers, G. 2006a. Thermal quality influence effectiveness of thermoregulation, habitat use, and behaviour in milk snakes. Oecologia **148**: 1-11.

Row, J.R. and Blouin-Demers, G. 2006b. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. Ecoscience **13**(4): 443-450.

Row, J.R. and Blouin-Demers, G. 2006c. Kernels are not accurate estimators of home-range size for herpetofauna. Copeia **4**: 797-802.

Row, J.R., Blouin-Demers, G., and Weatherhead, P. 2007. Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). Biological Conservation **137**(1): 117-124.

Row, J.R., Blouin-Demers, G, and Lougheed, S.C. 2012. Movements and habitat use of eastern foxsnakes (*Pantherophis gloydi*) in two areas varying in size and fragmentation. Journal of Herpetology **46**(1): 94-99.

Saumure, R.A. and Bider, J.R. 1998. Impact of agricultural development on a population of wood turtles (*Clemmys insculpta*) in Southern Québec, Canada. Chelonian Conservation and Biology **3**(1): 37-45.

Schaefer, W.H. 1934. Diagnosis of sex in snakes. Copeia **4**: 181.

Seburn, D., and Seburn, C. 2000. Conservation priorities for the amphibians and reptiles of Canada. World Wildlife Fund Canada and Canadian Amphibian and Reptile Conservation Network, Toronto, ON and Delta, BC. v + 93 pp.

Seburn, D. 2009. Recovery Strategy for the Eastern Hog-nosed Snake (*Heterodon platirhinos*) in Canada. *Species at Risk Act* Recovery Strategy Series. Parks Canada Agency, Ottawa, ON, 24 pp.

Semlitsch, R.D., and Bodie, J.R. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology **17**: 1219-1228.

Shine, R. 2003. Reproductive strategies in snakes. Proceedings of the Royal Society B **270**(1519): 995-1004.

Shine, R., Lemaster, M., Wall, M., Langkilde, and Mason, R. 2004. Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (*Thamnophis sirtalis parietalis*). Ecology and Society **9**(1): 9.

Smith, R. M., Spotila, J. R., and Bien, W. F. 2015. Spatial ecology of northern pinesnakes (*Pituophis m. melanoleucus*) in disturbed and undisturbed habitats in the New Jersey Pine Barrens. Herpetologica, **71**(1): 19-25.

Sperry, J.H., and Weatherhead, P.J. 2009. Does prey availability determine seasonal patterns of habitat selection in Texas ratsnakes? Journal of Herpetology **43**: 55-64.

Statistics Canada. 2017. Wasaga Beach, T [Census subdivision], Ontario and Ontario [Province] (table). Census Profile: 2016 Census. Statistics Canada Catalogue no. 98-316-X2016001. Statistics Canada, Government of Canada, Ottawa. Available from: https://www12.statcan.gc.ca/census-recensement/2016/dp-pd/prof/index.cfm?Lang=E [Accessed 18 February 2021].

Sullivan, B.K. 2012. Road Riding *In* Reptile Biodiversity: Standard Methods for Inventory and Monitoring. *Edited by* McDiarmid, R.W., Foster, M.S., Guyer, C., Gibbons, J.W., and Chernoff, N. Berkeley: University of California Press.

Sutton, W.B., Wang, Y., Schweitzer, C.J., and McClure, C.J.W. 2017. Spatial ecology and multi-scale habitat selection of the copperhead (*Agkistrodon contortrix*) in a managed forest landscape. Forest Ecology and Management **391**: 469-481.

Szerlag-Egger, S., and McRobert, S.P. 2007. Northern diamondback terrapin occurrence, movement, and nesting activity along a salt marsh access road. Chelonian Conservation and Biology **6**(2): 295-301.

Thomasson, V., and Blouin-Demers, G. 2015. Using habitat suitability models considering biotic interactions to inform critical habitat delineation: an example with the eastern hog-nosed snake (*Heterodon platirhinos*) in Ontario, Canada. Canadian Wildlife Biology & Management **4**(1): 1-17.

Tozetti, A.M., Oliveira, R.B., and Pontes, G.M.F. 2009. Defensive repertoire of *Xenodon dorbignyi* (Serpentes, Dipsadidae). Biota Neotropica **9**(3): 157-163.

Tozetti, A.M., Oliveira, R.B. 2010. Temperature preferences of *Xenodon dorbignyi*: field and experimental observations. Herpetological Journal **20**: 1-4.

Vanek, J.P., and Wasko, D.K. 2017. Spatial ecology of the eastern hog-nosed snake (*Heterodon platirhinos*) at the northeastern limit of its range. Herpetological Conservation and Biology **12**: 109-118.

Wallace, S.D. 2020. Wood turtle ecology and management strategies in a landscape under active agriculture. M.Sc. Thesis, Forestry and Environmental Management. University of New Brunswick, Fredericton, New Brunswick.

Watters, D. 2003. Wasaga Beach 2002 Building Activity Highest Yet. www.wasagabeach.com/business/index.html

Weatherhead, P.J., and Hoysak, D.J. 1989. Spatial and activity patterns of black rat snakes (*Elaphe obsoleta*) from radiotelemetry and recapture data. Canadian Journal of Zoology **67**: 463-468.

Weatherhead, P.J., and Prior, K.A. 1992. Preliminary observations of habitat use and movements of the eastern massasauga rattlesnake (*Sistrurus c. catenus*). Journal of Herpetology **26**(4): 447-452.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecological Society of America **70**: 164-168.

Wilson, R. 2004. Invasive Procedures Protocol for Snakes. Prepared for the Snake and Lizard Advisory Group.

World Wildlife Fund (WWF). 2016. Living Planet Report 2016: Risk and resilience in a new era. WWF International, Gland, Switzerland. 74 pp.

Yang, H., Zhao, L, Han, Q., and Fang, S. 2017. Nest site preference and fidelity of Chinese alligator (*Alligator sinensis*). Asian Herpetological Research **8**(4): 244-252.

Zagorski, G.M., Boreham, D.R., and Litzgus, J.D. 2019. Endangered species protection and evidence-based decision-making: Case study of a quarry proposal in endangered turtle habitat. Global Ecology and Conservation **20**: 1-9.

Zong, Y., Hu, B., Hall, B.G., Hogue, F., Xu, W., and Gao, X. 2020. A generalized linear mixed model approach to assess emerald ash borer diffusion. International Journal of Geo-Information **9**(7): 1-17.

Appendix 1A

Table 1.1 Categories and descriptions of general habitat types available for use by eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County, ON. Although bluff-side was also vegetated by forest habitat, the two were separated due to direct impacts of fluctuating hydrology from Lake Huron on the bluff-side.

General Habitat Type	Description
Crop	Planted cash crop and/or cover crop vegetation, area in use/recently used for agricultural purposes
Beach	Sand dune and dune grass dominant, along the shoreline of and highly influenced by the Great Lake system
Bluff-side	Transitional area from beach lowland to upland, adjacent to and directly influenced by Great Lake; includes vegetated and eroding portions of bluff-side
Closed-canopy Dominant Forest	Upland; deciduous, coniferous, and mixedwood dominant forested areas
Human Development	Marina, roads, paved surfaces, parking areas, residential/commercial/industrial/recreational infrastructure; does not include agricultural lands
Phragmites grass	Patch of *Phragmites australis australis*
Old Field	Once cleared for agriculture, now fallow and revegetating with predominantly herbaceous disturbance vegetation (ie. $\geq$ 50% non-native and some native re-establishment)
Open-canopy Sandy *Juniperus* Dominant	Upland; upper canopy absent/having large gaps, Juniperus dominant, and predominantly sandy substrate; characteristic preferred hog-nosed snake habitat (Platt 1969)
Riparian Area	Area near water source characterized by saturated soils and hydrophitic plant presence; does not include the riparian area of the Great Lake

Table 1.2 Sex, implantation date, date range(s) radio-tracked, number of radio-locations, mean distance per move (DPM; m), mean distance moved per day (DPD; m), and fate of eastern hog-nosed snakes (*Heterodon platirhinos*) radio-tracked from 2018 to 2020 in Huron County, ON.

Snake	Sex	Date Implanted	Range of Dates Tracked	Fate	Locations (#)	Average DPM ± SD	Average DPD ± SD
A	F	May 4, 2018	May 9, 2018 to July 23, 2018	Dead - Predated by mammal	36	124.4 ± 218.9	49.2 ± 81.2
B	F	May 4, 2018	May 9, 2018 to October 5, 2018	Dead - Euthanized post injury from unknown predator	61	111.5 ± 205.8	52.1 ± 82.9
C	M	May 11, 2018	May 15, 2018 to October 5, 2018	Dead - Predated by bird of prey	53	78.2 ± 164.0	27.9 ± 50.8
D	F	May 18, 2018	May 22, 2018 to October 30, 2018; January 24, 2019 to October 21, 2019	Unknown - Did not reappear (Apr 2020)	109	120.8 ± 192.3	39.9 ± 57.7
E	F	May 11, 2018	May 15, 2018 to June 13, 2018	Dead - Possible surgical complication	14	52.4 ± 80.8	21.8 ± 30.5
F	M	May 11, 2018	May 15, 2018 to October 30, 2018; January 24, 2019 to September 17, 2019	Unknown - Did not reappear (Apr 2020)	110	149.0 ± 253.7	57.6 ± 89.0
G	F	June 21, 2018	June 25, 2018 to October 30, 2018; January 24, 2019 to October 21, 2019; January 20, 2020 to July 7, 2020	Dead - Predated by mammal	120	82.8 ± 143.9	33.5 ± 56.4
H	M	June 28, 2018	July 3, 2018 to August 7, 2018	Dead - Hit by roadside mower	15	104.3 ± 114.2	47.4 ± 51.3
I	M	May 17, 2019	May 20, 2019 to October 21, 2019; January 20, 2020 to May 27, 2020	Dead - Hit by farm equipment	50	201.9 ± 319.6	62.1 ± 85.2
J	F	May 17, 2019	May 20, 2019 to October 21, 2019; January 20, 2020 to October 9, 2020	Live - Tracked to hibernation	118	84.0 ± 144.2	33.9 ± 55.0

Table 1.3 One-way analysis of variance (ANOVA) testing for sex effects by month on movement by eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County, ON. Distances moved per day (DPD) and distances per move (DPM) of radio-tracked snakes were recorded during the 2018 to 2020 active seasons, then log10-transformed and modelled as a function of sex (fixed effect).

log10-DPD

Month	# of Snakes	Statistical Outcome
April	3	$F_{(1,1)} = 54.79$, p = 0.09
May	9	$F_{(1,7)} = 0.028$, p = 0.87
June	9	$F_{(1,7)} = 2.095$, p = 0.19
July	9	$F_{(1,7)} = 0.14$, p = 0.72
August	8	$F_{(1,6)} = 0.028$, p = 0.87
September	7	$F_{(1,5)} = 0.232$, p = 0.65
October	7	$F_{(1,5)} = 0.002$, p = 0.97

log10-DPM

Month	# of Snakes	Statistical Outcome
April	3	$F_{(1,1)} = 61.33$, p = 0.08
May	9	$F_{(1,7)} = 0.089$, p = 0.77
June	9	$F_{(1,7)} = 3.597$, p = 0.10
July	9	$F_{(1,7)} = 0.598$, p = 0.47
August	8	$F_{(1,6)} = 0.141$, p = 0.72
September	7	$F_{(1,5)} = 0.167$, p = 0.70
October	7	$F_{(1,5)} = 0.007$, p = 0.94

Table 1.4 Area proportions (%) of available habitat types, proportions (%) of eastern hog-nosed snake (*Heterodon platirhinos*) radio telemetry relocations of within habitat types, and average distances between habitat types and all telemetry relocation points (used, n = 689; random, n = 689) in Huron County, ON from 2018 to 2020.

Habitat Type	Proportion of Total Area (%)	Proportion of Observation Locations (%)	Average Distance to Habitat from Point (m)	
			Used	Random
Agricultural	27.1	2.1	397.4	170.5
Beach	1.6	24.2	348.9	755.0
Bluff-side	5.2	20.3	732.7	1095.8
Closed-canopy Forest	21.4	18.8	46.9	105.4
Human Development	28.3	7.5	67.0	58.1
Old Field	4.5	7.2	150.8	165.8
Open Sandy Juniper	0.8	3.4	363.0	606.2
Phragmites	0.05	0.6	NA	NA
Riparian	10.6	16.6	219.9	214.9

Table 1.5 A generalized linear mixed model with a Gamma distribution evaluating snake occurrence (binary) at the landscape scale as a function of predictors representing distance to specified habitat types (from location and random points). A total of 128 models were fit for all possible predictor combinations; only the null model and top models with ΔAICc ≤ 2 are shown. The Akaike's Information Criterion value (AICc) difference from top model in AIC score (ΔAICc), Akaike weights, and number of parameters (K) of the models are included. Estimates, standard errors (SE), are presented for the model parameters after model averaging had been performed.

General Habitat Model (Landscape) Formula	K	AICc	ΔAICc	Weights
Occurrence ~ Intercept	1	3101.59	813.76	1.26E-177
Occurrence ~ Beach + Bluff + Crop + Forest + Human + Old Field + Riparian	8	2287.83	0.00	0.65
Occurrence ~ Beach + Bluff + Crop + Forest + Human + Old Field	7	2289.08	1.25	0.35

Top Model Variables (Landscape)					
	Parameter	Estimates	SE	Lower 85% CI	Upper 85% CI
Model Averaging	(Intercept)	-1.66	0.07	-1.76	-1.55
	Beach	-2.31	0.17	-2.55	-2.07
	Bluff	0.61	0.15	0.39	0.82
	Crop	2.17	0.15	1.95	2.38
	Forest	-0.60	0.19	-0.88	-0.32
	Human	0.97	0.13	0.78	1.16
	Old Field	-0.60	0.15	-0.82	-0.37
	Riparian	0.18	0.18	0.06	0.50

Table 1.6 A generalized linear mixed model with a Gamma distribution evaluating snake occurrence (binary) at the home range scale as a function of predictors representing distance to specified habitat types (from location and random points). A total of 64 models were fit for all possible predictor combinations; only the null model and top models with ΔAICc ≤ 2 are presented. The Akaike's Information Criterion value (AICc) difference from top model in AIC score (ΔAICc), Akaike weights, and number of parameters (K) of the models are included. Estimates, standard errors (SE), are presented for the model parameters after model averaging had been performed.

General Habitat Model (Home Range) Formula	K	AICc	ΔAICc	Weights
Occurrence ~ Intercept	1	3038.61	272.19	5.07E-60
Occurrence ~ Beach + Bluff + Crop + Forest + Old Field + Riparian	7	2766.42	0.00	0.65

Top Model Variables (Home Range)				
Parameter	**Estimates**	**SE**	**Lower 85% CI**	**Upper 85% CI**
(Intercept)	-1.25	0.05	-1.32	-1.18
Beach	-0.30	0.13	-0.48	-0.11
Bluff	1.57	0.14	1.38	1.77
Crop	2.09	0.16	1.86	2.32
Forest	-0.39	0.13	-0.58	-0.20
Old Field	-0.71	0.14	-0.92	-0.51
Riparian	0.35	0.17	0.11	0.59

Appendix 1B

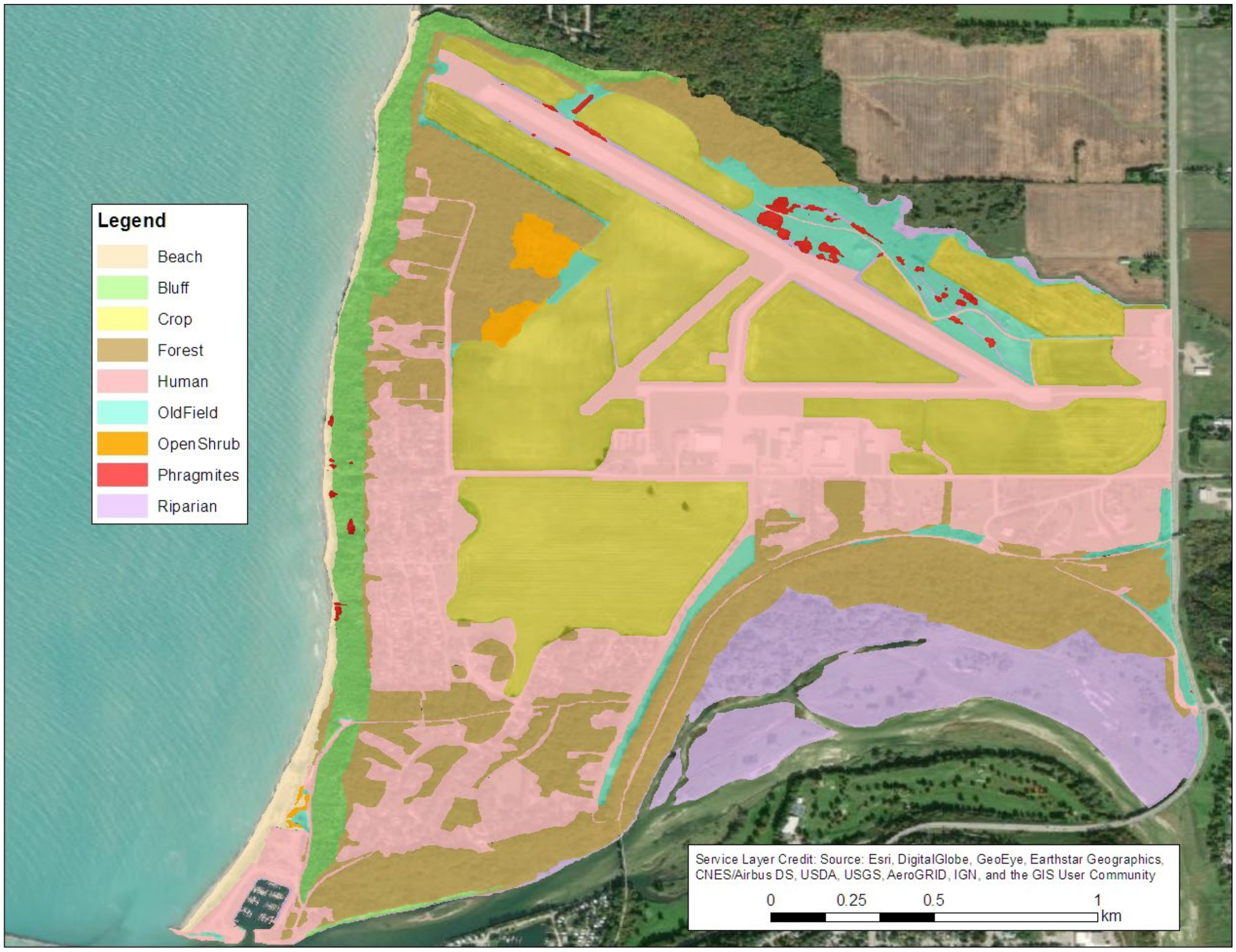

Figure 1.1 Habitat types available for use by eastern hog-nosed snakes (*Heterodon platirhinos*) within Huron County, ON. Habitat polygons were digitized and delineated in ArcMap (v. 10.5.1; ESRI 2021) by referencing aerial imagery (0.2 m^2 resolution, Huron County 2015; CNES 2020).

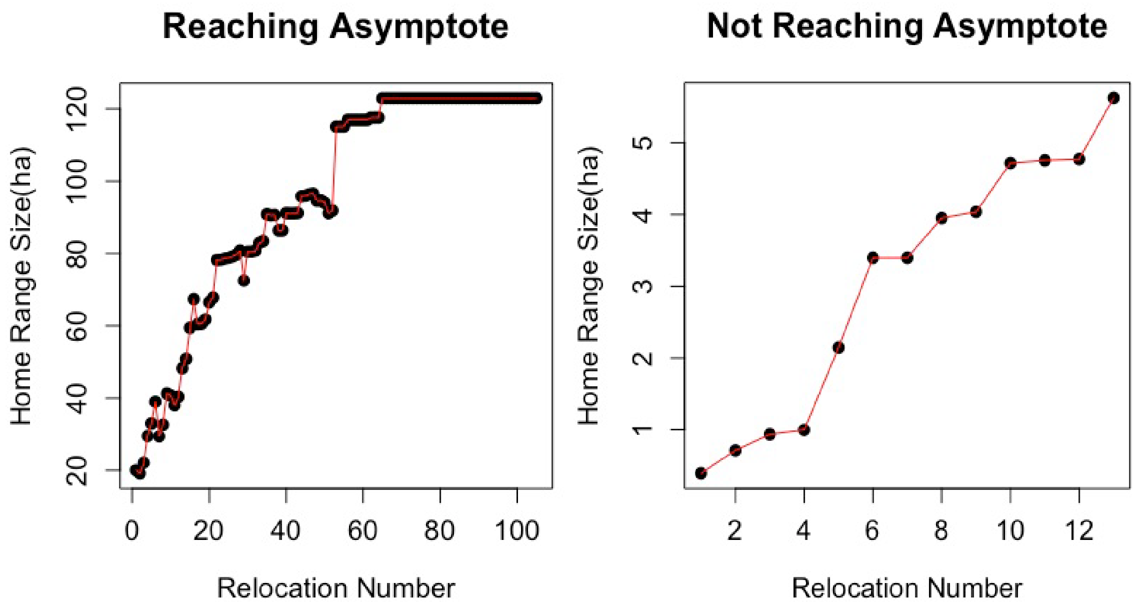

Figure 1.2 Examples of snake home range size estimates (ha) reaching asymptote (left) and not reaching asymptote (right; snake not included in home range analyses) with increasing number of radio-locations.

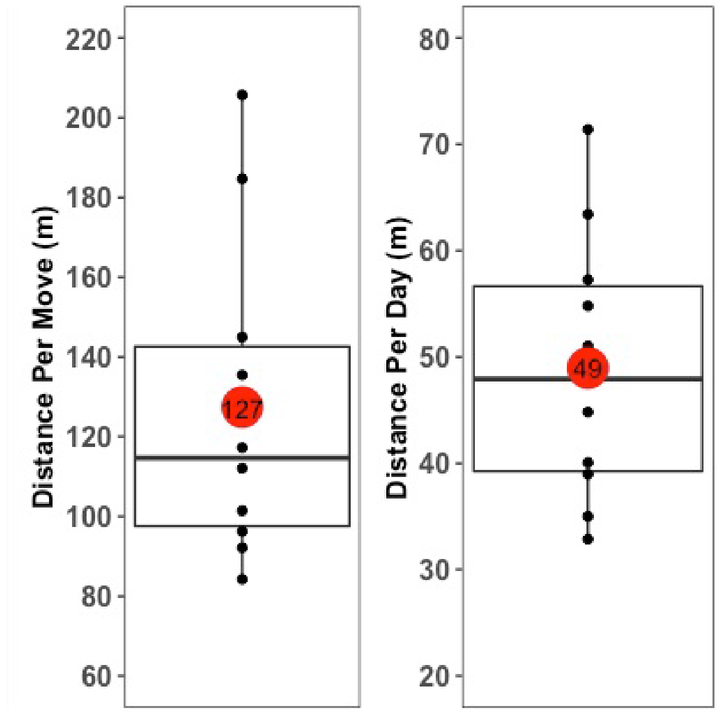

Figure 1.3 Mean distance per move (DPM, m) and distance moved per day (DPD, m) during the active season (April – October) for radio-tracked eastern hog-nosed snakes (*Heterodon platirhinos*; n = 10) in Huron County, ON. Boxes represent 25th to 75th percentiles; solid line within each box represent medians; whiskers represent ranges; red circles and associated numbers represent the means of all radio-tracked snakes, and the black circles represent means of each individual snake.

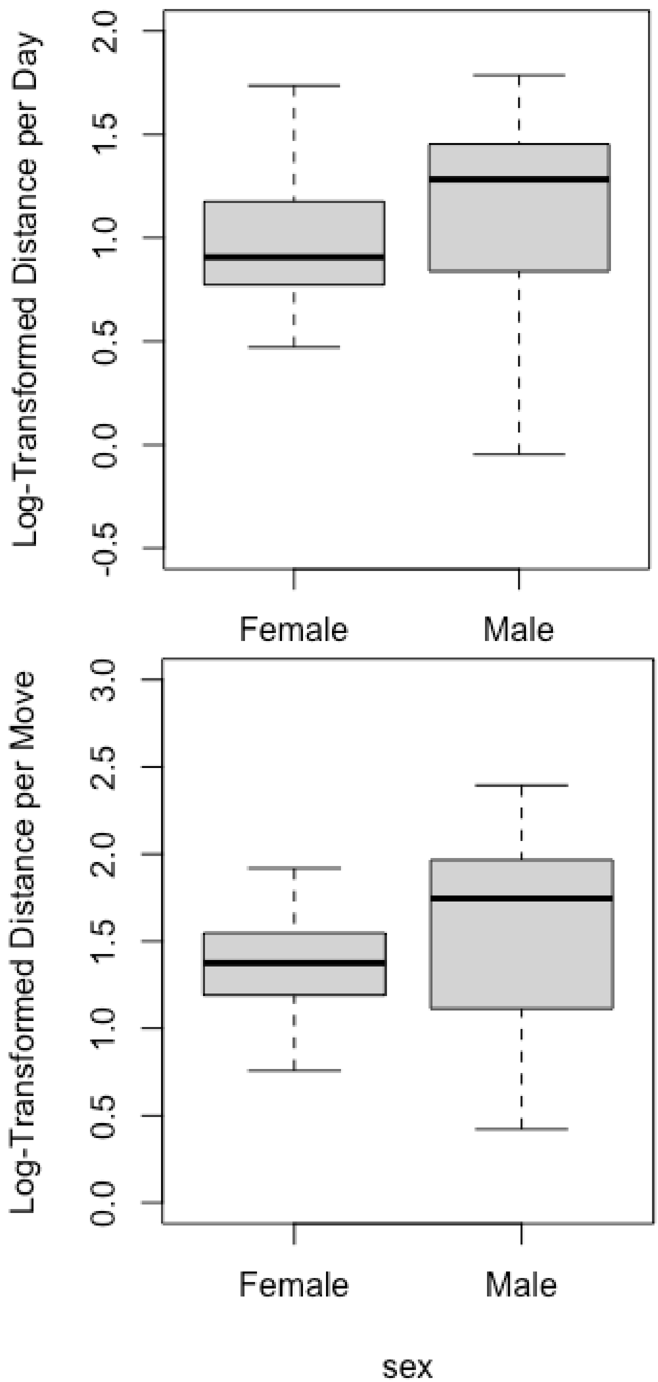

Figure 1.4 Distance per day (top panel) and distance per move (bottom panel) from 2018 to 2020 of male (4 snakes, 228 radio-locations) and female (gravid and non-gravid combined, 6 snakes, 453 radio-locations) eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County, ON. Boxes represent 25th to 75th percentiles; solid lines within each box represents medians; whiskers are ranges.

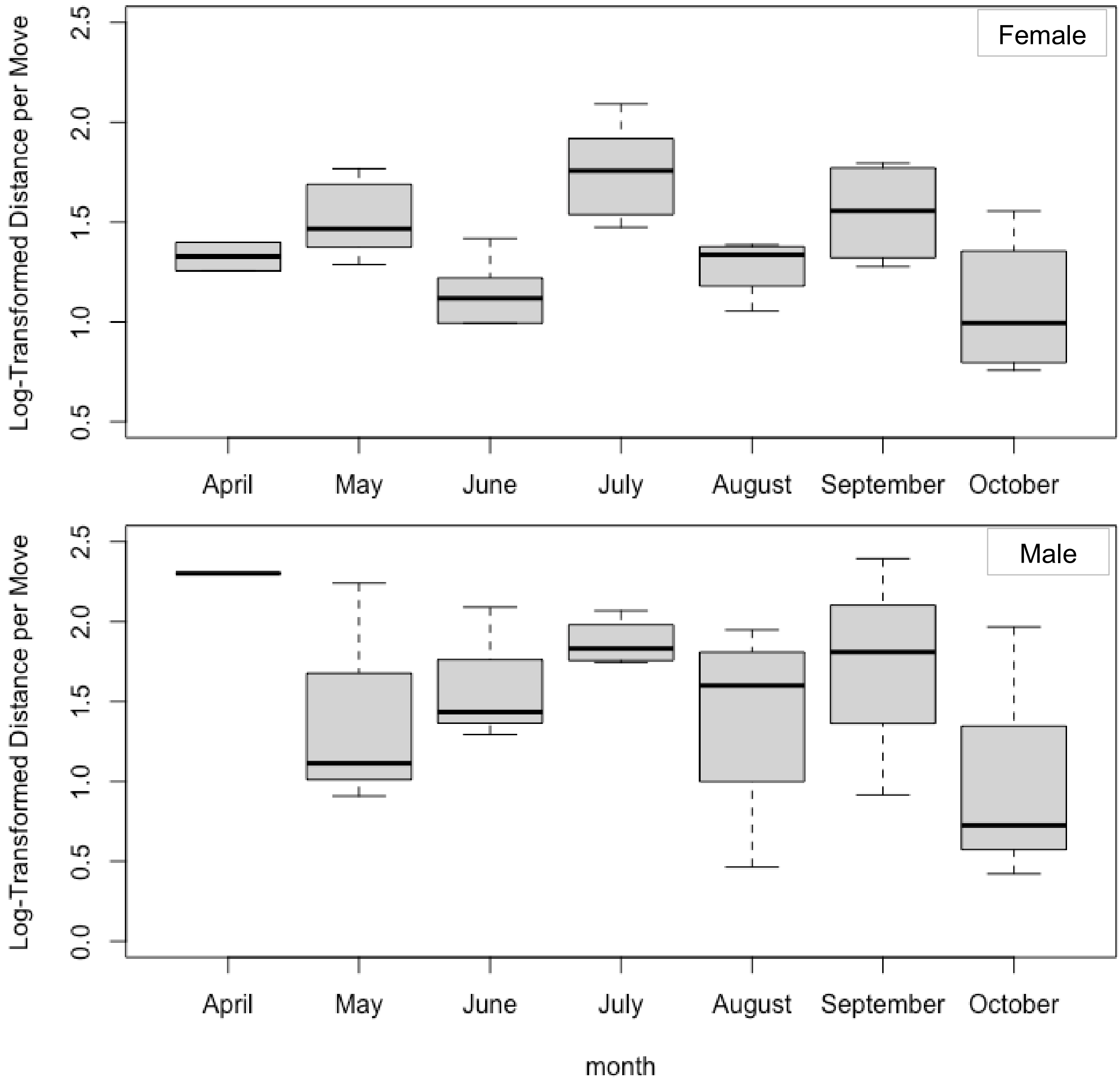

Figure 1.5 Monthly distance per move for female (top panel; gravid and non-gravid combined, 6 snakes, 453 radio-locations) and male (bottom panel; 4 snakes, 228 radio-locations) eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County, ON from 2018 to 2020. Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

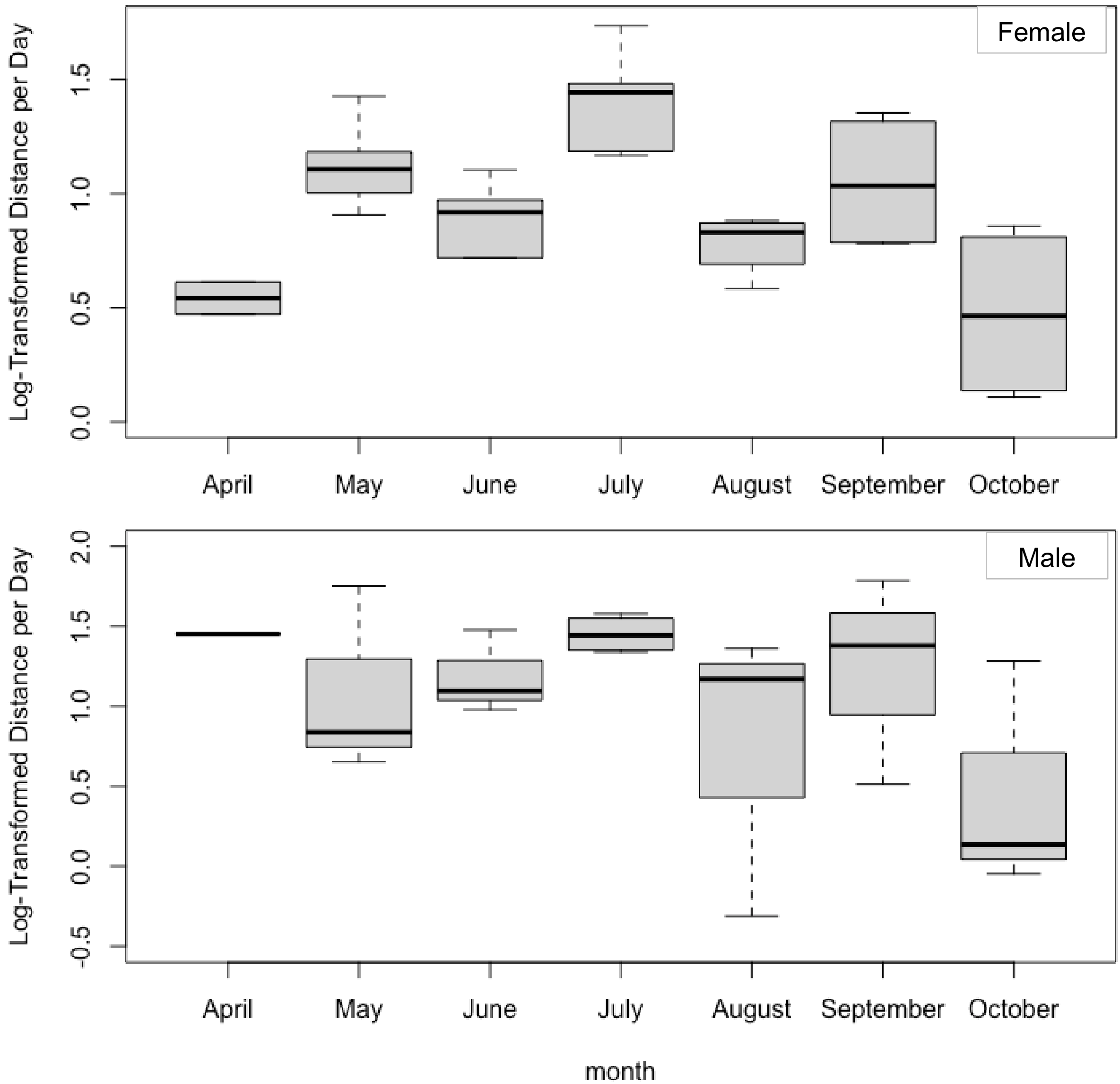

Figure 1.6 Monthly distance per day for female (top panel; gravid and non-gravid combined, 6 snakes, 453 radio-locations) and male (bottom panel; 4 snakes, 228 radio-locations) eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County, ON from 2018 – 2020. Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

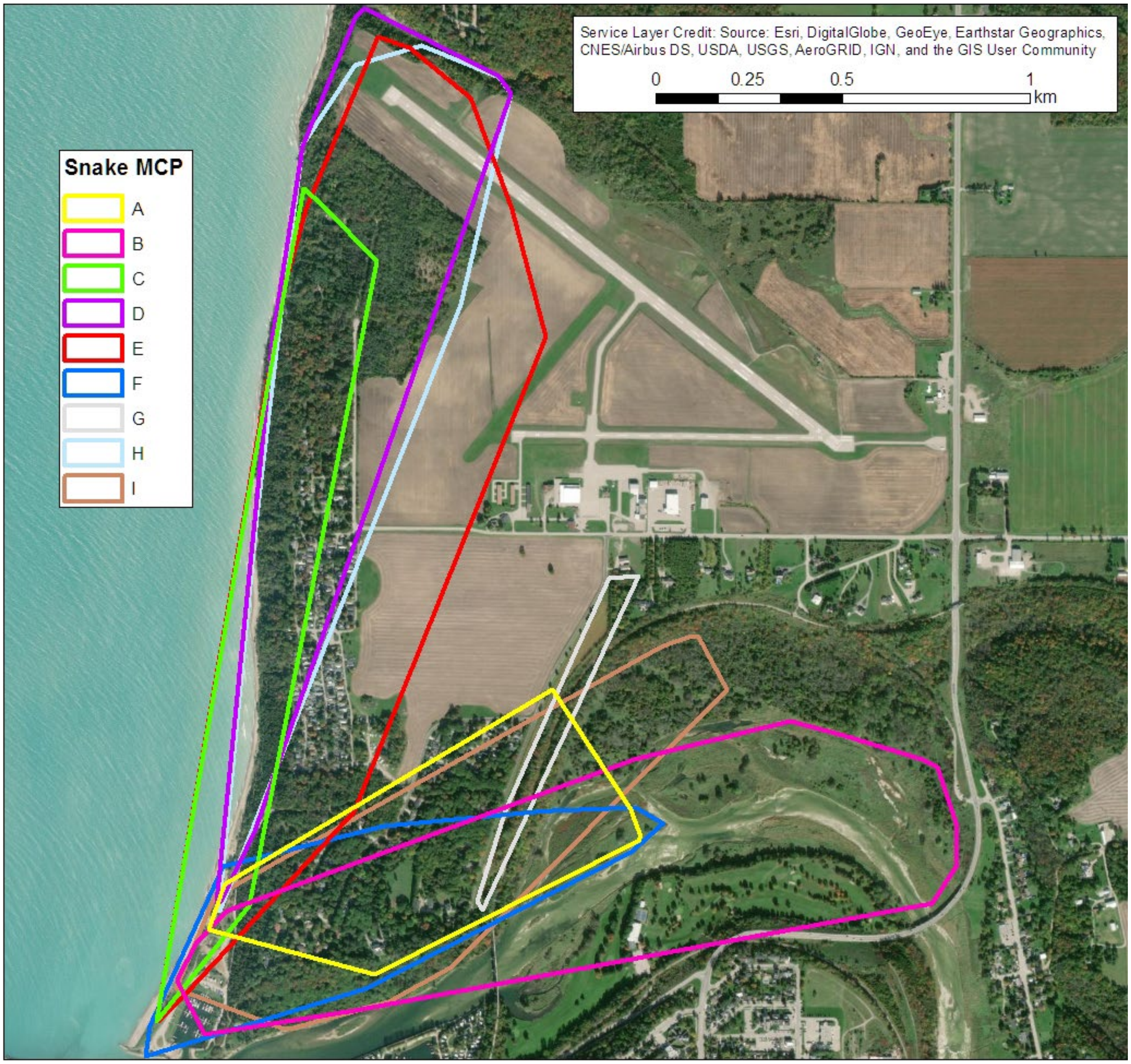

Figure 1.7 Boundaries of Minimum Convex Polygon home ranges (MCP drawn in ArcMap using the minimum bounding geometry tool—convex hull (auto-calculated at 100%; ESRI 2021)) for eastern hog-nosed snakes (*Heterodon platirhinos*; n = 9; individual snakes are indicated by different letters) in Huron County, ON.

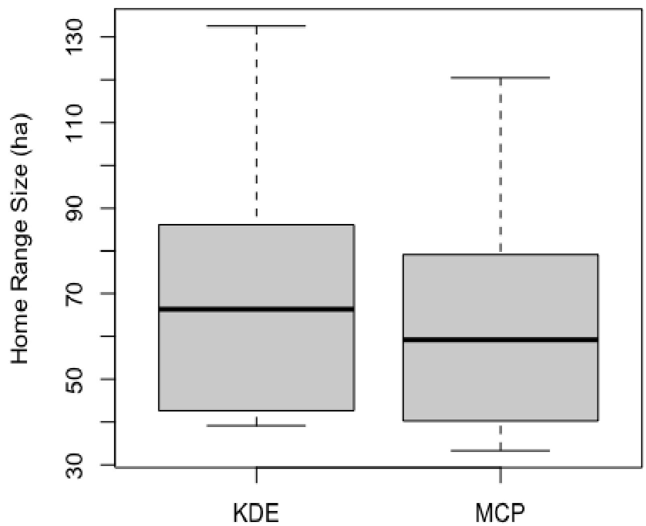

Figure 1.8 Kernel Density Estimate (KDE; 95%) and Minimum Convex Polygon (MCP; 95%) home range size estimates (ha) of radio-tracked eastern hog-nosed snakes (*Heterodon platirhinos*; n = 8, sexes combined) recorded in Huron County, ON from 2018 to 2020. Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

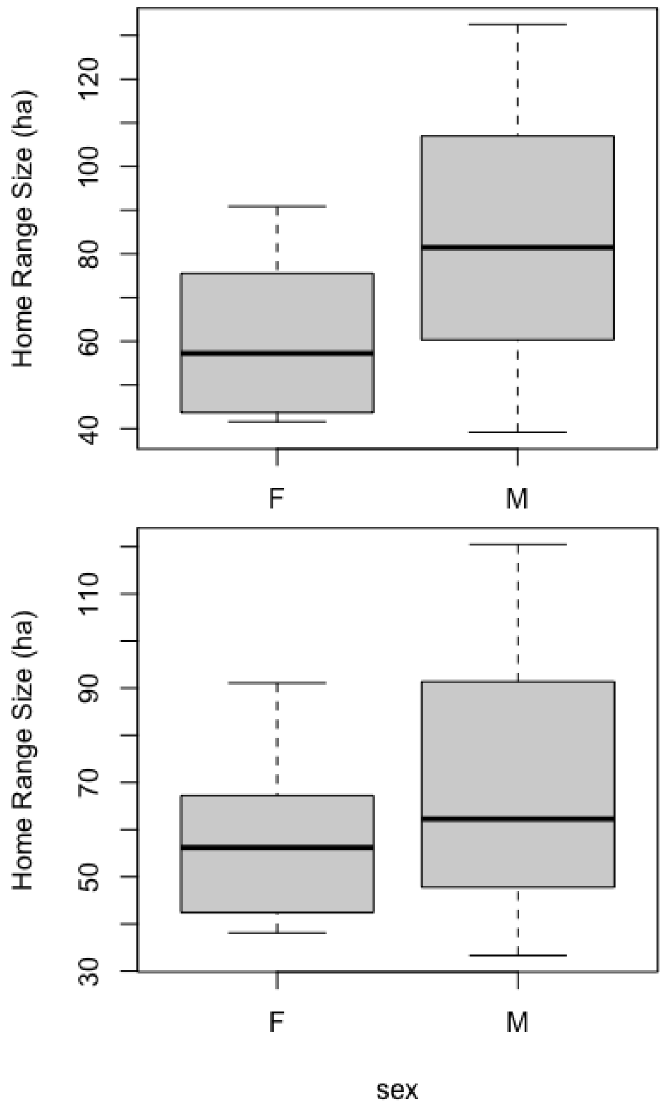

Figure 1.9 Minimum Convex Polygon (MCP; 95%; top panel) and Kernel Density Estimate (KDE; 95%; bottom panel) home range sizes (ha) of radio-tracked male (M; n = 4) and female (F; n = 6; gravid and non-gravid individuals combined) eastern hog-nosed snakes (*Heterodon platirhinos*; n = 8) in Huron County, ON from 2018 – 2020. Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

Chapter 2: EVALUATING FACTORS THAT MAY INFLUENCE THE FITNESS OF EASTERN HOG-NOSED SNAKES INHABITING A HIGHLY MODIFIED LANDSCAPE

Abstract

Populations at range peripheries often face ecological challenges that exacerbate existing threats. In southwestern Ontario, critical habitat for the threatened eastern hog-nosed snake (*Heterodon platirhinos*) faces various competing land uses, presenting the need to quantify habitat selection and threats to critical habitat to ensure persistence of at-risk populations. I investigated whether a highly modified landscape within Huron County, Ontario influenced thermal habitat quality, habitat selection, and snake fitness proxies. In 2019 and 2020, habitat variables at local (within 15 m) and exact scales (within 1 x 1 m plot) were quantified at relocations of 10 radio-tracked snakes. Each used site was paired with a random plot (n = 231 paired plots) to assess habitat use versus availability. To determine variables influential to habitat use, a resource selection function (RSF) was used to create and rank (using Akaike's Information Criterion for small sample sizes (AICc)) model combinations (snake occurrence ~ structural habitat variable). Snake occurrence was negatively associated to overhead canopy (%) at both scales), followed by negative association with distance to shrub and positive associations with vegetation density and distance to reed canary at the localized scale, and positively associated presence of cover at the exact scale. Thermal habitat quality was quantified from hourly ground temperatures (°C) of invasive grasses and representative habitats and compared using Kruskal-Wallis and Dunn's post-hoc analyses; I found that thermal quality varied among habitat types and grass species. As a proxy for fitness, body condition was inferred from residuals of a body mass on snout-vent length regression and showed that Huron County snakes were heavier and in better condition compared

to conspecific populations. To persist within Huron County's modified landscape, hog-nosed snakes appear to select small, thermally suitable, and structurally complex patches within modified habitats. While proxies of fitness in Huron County snakes do not appear imminently impacted by disturbance, modification threatens critical habitat and should be monitored and protected to ensure population persistence.

Introduction

Populations inhabiting range peripheries are often scarce, isolated, and contain fewer individuals (Levin 1970; Lawton 1993; Lesica and Allendorf 1995), limiting their resilience to rebound from population declines caused by stochastic events (Lesica and Allendorf 1995; Frankham 1996; Hecnar 1997). Canada's thermally challenging climate can be a limiting factor for reptile populations at the northern extent of their range (Picard et al. 2011; Martino et al. 2012; Lesbarrères et al. 2014; COSEWIC 2019). However, thermoregulatory challenges are not the only threats to reptiles in Canada, where over three quarters of species are listed as at risk of extinction (COSEWIC 2019) largely due to increased urban sprawl, resource-exploitation, and land-use changes (Sala et al. 2000; Walther et al. 2002; Lesbarrères et al. 2014). In southern Canada, diverse areas for Canadian herpetofauna (Lesbarrères et al. 2014; COSEWIC 2019) overlap with intensive anthropogenic activity (Kerr and Cihlar 2003). Thus, there is potential for conflict between human demand and conservation of herpetofauna in southern Canada, and therefore a thorough understanding of species' habitat preferences and thermal ecology are important aspects of the recovery process.

Anthropogenic disturbance can impact reptile fitness. Traditionally, biological fitness is understood under the context of an organism's survival, contribution of offspring, and the efficiency of resource use for reproduction and survival (Brown et al. 1993; Weatherhead and Brown 1996). While they may not directly measure survival or reproductive output, proxies of fitness can act as valuable tools to infer fitness. Body size and body condition are often applied as proxies of individual fitness, where larger body sizes and better body condition are presumed linked to reproductive success (Litzgus and Brooks 1998; Iglesias-Carrasco et al. 2016; Wilder et al. 2016). For example, female spotted turtles (*Clemmys guttata*) with better body condition produce heavier clutches and larger sized eggs (Litzgus et al. 2008), and larger sized females produce larger clutch sizes (Litzgus and Brooks 1998). In snakes, body condition and size also correlate with reproductive success, where the proportion of breeding females in some species positively correlates to snout-vent length (SVL; Reading 2004) and body condition (Diller and Wallace 1984; Naulleau and Bonnet 1996; Reading 2004). Human activity is known to influence reptile behaviour, body condition, somatic growth, reproduction, and mortality (Parent and Weatherhead 2000; Burger 2001; Endriss et al. 2007; Wolf et al. 2013; Lomas et al. 2015; Walkup et al. 2017). For example, reptiles are often killed on roads during dispersal to acquire resources (Andrews et al. 2008; Mccardle and Fontenot 2016; Choquette and Valiant 2016). While the transformation of natural habitats can negatively impact reptile fitness, modification can create suitable habitats, but their use can incur potentially fatal costs. For example, edge habitats such as transition areas between forests and agricultural fields can be thermally suitable for reptiles (Blouin-Demers and Weatherhead 2001a; Row and Blouin-Demers 2006a) but can also present an increased risk of predation (Hansen et al. 2019). Thus, while some reptiles may avoid or abandon certain human-modified areas, some may remain within the disturbance (Brown 1993; Moore and Seigel 2006; Ettling et al. 2013), demonstrating that species presence/absence is not a reliable indicator of tolerance or acclimation to anthropogenic activity (Lomas et al. 2015). Reptiles that remain within human-modified areas often exhibit differences from those that avoid modified areas, including slower growth rates, poorer body condition, increased mortality, or compromised offspring viability (Jenkins et al. 2009; Lomas et al. 2015; Hansen et al. 2019; Putman et al. 2019)—crucial aspects that can negatively impact overall fitness and may be missed by presence/absence surveys alone.

The acquisition of resources is critical for the success of reptiles to carry out basic life requirements, with the distribution and availability of such resources playing key roles in reptile habitat selection. For reptiles, behaviour is largely driven by thermoregulatory needs (Mullin and Seigel 2009) and meeting such needs relies on the quality and availability of thermal resources throughout the landscape. Habitat selection can be organized into a hierarchy of different orders (Johnson 1980) and is influenced by resource acquisition and availability across the landscape. Availability of thermal resources largely falls within the fourth order of selection (Johnson 1980). General habitat types within an organism's home range constitute the third order of habitat selection, while the resources within the habitat types comprise the fourth order (Johnson 1980). As thermal quality is a consistent factor in squamate microhabitat selection (Blouin-Demers and Weatherhead 2001b; Shoemaker and Gibbs 2010; Lelièvre et al. 2011), thermal landscape integrity can be crucial to population persistence.

Introductions of non-native vegetation, such as exotic grasses, threaten resource availability and ability to thermoregulate as proliferation can impact structural and thermal qualities of critical habitat (Weinstein and Balletro 1999). When exotic grass species colonize once-open areas such as sandy coastal shores (OMNR 2011; Markle et al. 2018; LHCCC 2019) or savanna and meadow habitats (Markle et al. 2018), attempts to control them (cutting, burning, rolling, hand-pulling, grazing, tarping, and chemical applications [e.g., glyphosate herbicides]; OMNR 2011; Anderson 2012) can require intensive management with no guarantee of long-term restoration success (Blossey and McCauley 2000; Martin and Blossey 2013; Quirion et al. 2018). In southern Ontario the exotic grass species, *Phalaris arundinacea* (reed canary grass) and *Phragmites australis australis* (herein *Phragmites*) are examples of invasive plants drastically altering native habitats.

The eastern hog-nosed snake (*Heterodon platirhinos*) is one of 10 snake species-at-risk that inhabit the human-modified landscape of southern Ontario (COSEWIC 2019). To date, critical habitat necessary for the recovery and survival (Statutes of Canada 2002) of this threatened species has not yet been identified (Kraus 2011; OMNRF 2016a; COSEWIC 2021). However, a unique and well-known habitat requirement for eastern hog-nosed snakes is loose or sandy soils, required for nesting and over-wintering activities (Cunnington and Cebek 2005; COSEWIC 2007). While other studies have examined habitat preferences in northern populations of eastern hog-nosed snake (Cunnington 2004; Lagory et al. 2009; Robson 2011; Goulet et al. 2015; Buchanan et al. 2017; Vanek and Wasko 2017), they did not address the potential impacts of invasive plants on habitat thermal quality. In addition, snake habitat selection is known to vary amongst populations (Benson and Chamberlain 2007; Edkins et al. 2018), and because habitats used by eastern hog-nosed snakes often overlap with densely human-populated areas in southern Ontario (COSEWIC 2007), their survival can be compromised. For example, near Wasaga Beach, ON snakes are surrounded by subdivisions and municipal infrastructure (Cunnington pers. comm.), and the threat of human-snake interaction is so severe that if a snake ventures out of protected areas, they have approximately 24 hours to return to protected habitat or their chance of survival drops close to zero (Cunnington pers. comm.). Eastern hog-nosed snakes in Huron County, ON also inhabit a modified landscape with widespread anthropogenic activity (Chapter 1), and may experience compromised survival and fitness (e.g., smaller body sizes and poorer body condition). Thus, the overall goals of my second chapter were to quantify fourth order habitat selection (Johnson 1980) by eastern hog-nosed snakes and to assess impacts of human activity and invasive plants on habitat thermal quality and snake fitness. As thermal quality is a consistent factor in squamate microhabitat selection

(Blouin-Demers and Weatherhead 2001b; Shoemaker and Gibbs 2010; Lelièvre et al. 2010 & 2011), availability and accessibility to high quality thermoregulatory habitat will be important to population persistence for eastern hog-nosed snakes.

Hypothesis and Predictions

Anthropogenic activity will negatively impact fitness proxies (e.g., body size and condition) and direct measures of fitness (e.g., mortality), and thermal habitat quality. If human modified areas are unsuitable habitat for eastern hog-nosed snakes, then:

1) Habitat selection will not be random and snake presence will be positively associated with variables that provide refuge from biotic and abiotic threats.
2) Due to shading by dense vegetation, areas colonized by invasive grasses will have cooler ground temperature profiles and be unsuitable thermal habitat compared to other natural habitat types. Thus, invasive grass patches will be negatively associated with snake use.
3) Snakes in Huron County will have smaller body sizes, poorer body condition, and higher mortality rates than conspecific populations near Point Pelee, ON inhabiting more natural habitats.

Materials & Methods

Study Site

Data were collected within Huron County, Ontario, Canada (Latitude: 43° 38’ 41”, Longitude: -81° 41’ 25”), located within the mixed-wood plains ecozone (OMNRF 2018). Two major water systems, the Maitland River and Lake Huron, and a variety of soil types (i.e., sandy lakeshore and agriculturally suitable soils) drive the local economy through agriculture, tourism, and lakeshore recreation (Hoffman et. al 1952; Cummings et al. 1998; OMNRF 2018). The area consists of a diversity of habitat types including cropland, anthropogenic infrastructure (e.g., small municipal airport, marina, residential housing), and natural areas (e.g., steep lakeshore bluffs, forest, Lake Huron shoreline, juniper shrubland; Fig. 2.1; Chapter 1). Above the lakeside bluffs, much of the area has been cleared for seasonal and permanent residences, while density of infrastructure along the shoreline and river valley is low.

Structural Habitat

Snakes implanted with radio transmitters were tracked 2-5 x/week during the active season (April to September) using a Yagi-antenna and Advanced Telemetry Systems (ATS) receiver (4 MHz frequency range; Model R410; Isanti, Minnesota). Radio transmitters (Sigma8, Aurora, Ontario) were surgically implanted by Dr. Sean Egan (Egan-Fife Animal Hospital, Chatham, Ontario), approved under AUP #19-386, and followed snake surgical procedures outlined by Wilson (2004) and Crawshaw and Lentini (2013). To comply with maximum transmitter mass to body mass ratio of 0.05:1 dictated by the animal care protocol, radio transmitters (I-450 Model, mass = 8.5 g) were implanted into body cavities of non-gravid (at time of implantation) female snakes and male snakes with a mass >200 g. Location coordinates and habitat survey data of radio telemetry locations post-surgery were recorded on a Samsung Galaxy tablet equipped with a GPS amplifier (EOS Tools Pro; ±1 m accuracy) using Survey123 (ESRI 2021).

I completed habitat surveys at radio telemetry locations in paired used-available plots to determine variables important to third and fourth order habitat selection (Johnson 1980). During the 2019 and 2020 active seasons habitat quantification surveys were completed within 14 days of identifying a radio location and after a snake had left the location (to avoid stepping on, or disturbing, the snake). To represent ‘available’ habitat on the landscape, sites were chosen based on randomly generated bearings (1 - 360°) and number of steps (1 - 50 steps), following methods used by Blouin-Demers and Weatherhead (2001c), Compton et al. (2002), and Row and Blouin-Demers (2006b), as well as to work within constraints of the landscape (i.e., Lake Huron, Maitland River, human development). The same habitat variables were measured at 'used' sites and 'available' sites and recorded at two scales: a local scale within a 15 m radius (Matlack 1993; Murcia 1995; Row and Blouin-Demers 2001a) of the snake telemetry location (Table 2.1) and at the exact location where the snake was observed (within a 1 x 1 m square plot centered on the location; Table 2.2 and 2.3). At the exact location scale, vegetation variables were recorded by growth-form and height (Table 2.3), in addition to recording variables in two- and three-dimensional views (2-D and 3-D, respectively; Table 2.2) to encapsulate layers of habitat complexity. The 2-D view represented a strictly overhead view (e.g., % cover by big leafy branch), while 3-D view capture the layers 'hidden' beneath the overhead view (e.g., % cover of big leafy branch and % cover of leaf litter beneath leafy branch). Presence and density (Table 2.4; Adams et al. 2016) of invasive grasses, *Phragmites australis australis* (*Phragmites*) and *Phalaris arundinacea* (reed canary grass) were also recorded (Saltonstall and Hauber 2007; King County 2010; OFAH/OMNRF 2012; OIPC 2019). Resource selection function (RSF) models (Johnson 1980; Manly et al. 2002) were created and used to determine which habitat variables influenced snake habitat selection. The models evaluated whether snake occurrence (a binary factor) was predicted by multiple factors, structural habitat variables (from used and available sites). Although habitat selection at local and exact location scales were modelled separately, steps to create models were the same for both scales. Predictor variables were analyzed to identify if any pairs were strongly correlated (Pearson correlation > 0.6) at either habitat scale. Any covariates that were correlated were then run through univariate models, with variables that performed best (based on AIC scoring comparison) retained and later included in a global model (snake occurrence ~ structural habitat variable). To create the models the coxph function in the 'survival' R package was used (Therneau 2022). All possible predictor combinations of the global model were then ranked using Akaike Information Criterion corrected for small sample sizes (AICc; Hurvich and Tsai 1989; Burnham and Anderson 2002), where models with ΔAICc <2 were considered the best at explaining variance in snake occurrence at the local or exact location habitat selection scales.

Thermal Habitat

To create thermal profiles of available habitat types, temperature data loggers (Thermochron iButton DS1921G-F5 Series, accuracy ± 1°C) were deployed to record hourly ground temperatures. During the 2019 and 2020 active seasons (May to September), data loggers were deployed at 77 different locations amongst 10 thermal habitat types (Table 2.5). Thermal suitability of invasive grasses was assessed by grass species and whether stands were alive or dead (e.g., standing dead vegetation post-herbicide application; Table 2.5). As a fail-safe, two temperature data loggers were attached to flagging tape, then tied and secured to a sturdy object (e.g., a shrub, base of *P. arundinacea* bunched together), and laid upon the ground surface face-side (serial number information) down. Because portions of the study site frequently experienced human activity, iButtons were thoughtfully placed out of sight, to discourage removal or tampering. To test for differences in ground temperatures (mean ± SD) among habitat types, the non-parametric equivalent to one-way ANOVA, Kruskal-Wallis (KW; *H*-statistic) test and Dunn's post-hoc test were used, as the data were not normally distributed.

Proxies of Individual Snake Fitness

Visual encounter surveys (VES) and radio telemetry were the primary methods used to actively survey for snakes over 3 field seasons (2018 – 2020). VES followed snake species-at-risk survey protocols (>10 surveys in an active season; OMNRF 2016b) and began in mid-April around the expected time of emergence from hibernation. Generally, a team of 1 to 2 people conducted VES 4 – 7 times per week when air temperature was between 10 and 30°C (Casper 2001; EMRT 2005; Harvey 2008). While walking in areas of suitable habitat (i.e., dune and forested areas; OMNRF 2016b) and areas with previously reported sightings, surveyors simultaneously examined the ground surface and beneath potential cover objects (e.g., shrub, driftwood; OMNRF 2016b) for snakes. As vegetation became denser and radio telemetry work increased, VES effort became less frequent. VES effort increased again in late June/early July around the expected nesting season and were concentrated within a known nesting area (unpublished report, Huron Stewardship Council) in an effort to capture new females. Nesting area searches occurred when temperatures were slightly cooler (sunrise to 09:00 and 17:00 to sunset), to coincide with optimal mean nesting temperature for *H. platirhinos* (24°C; Peet-Paré and Blouin-Demers 2012). Mark-recapture was used to identify new or previously caught individuals; all snakes >30 g were subcutaneously implanted using a syringe injector with a Passive Integrated Transponder (PIT) tag (within the lower third of the venter and anterior to the cloacal scales; Leuenberger et al. 2019). Demographic data including age class (neonate, juvenile, sub-adult, adult), sex, individual identification (PIT-tagged), and whether an individual was alive or dead (with cause of death if possible) were recorded during VES surveys and incidental observations. These data were then used to describe the population structure of eastern hog-nosed snakes in Huron County observed from 2017 to 2020, and to estimate minimum mortality rate (total # of deceased individuals observed/total # of individuals encountered) from 2018 to 2020.

Morphometric measurements, including body mass and snout-vent length (SVL) were collected upon first capture and subsequent recaptures, and used to create a body condition index. Body mass ad SVL were first log(10)-transformed, then used in a log-transformed body mass on log-transformed SVL regression, and the residuals of the regression were then used to create a body condition index (Weatherhead and Brown 1996; Somers et al. 2011). Positive residuals of the regression indicated relatively good condition, while negative residuals were indicative of relatively poor condition (Litzgus et al. 2008; Somers et al. 2011). Mann-Whitney U-tests (for non-normally distributed data) and t-tests (normally distributed data) were used to compare body morphometrics (mean ± SD) and condition of adult and sub-adult (>50 cm; Harding 1997) hog-nosed snakes, separated by sex, from Huron County with data from populations near Point Pelee, ON, in a less human-modified landscape (data provided by S. Gillingwater 2021, Thames River Conservation Authority).

Results

Structural Habitat

A total of 462 habitat surveys were completed from 2018 to 2020 at 231 paired used-available locations of 12 unique radio-telemetered snakes. The HSC completed 106 habitat surveys at 53 locations from 10 radio-telemetered snakes in 2018, while 280 surveys (140 locations) were done in 2019 from 5 radio-tracked individuals (2 unique snakes, 3 also tracked in 2018), and 76 (38 locations) were completed in 2020 from locations of 3 radio-tracked snakes (also tracked in 2019).

At the local scale (15 m), reed canary density was strongly correlated with distance to reed canary (r = 0.63), and *Phragmites* density was highly correlated with distance to *Phragmites* (r = 0.70). When run as separate univariate models, *Phragmites* density (ΔAICc = 0.00) outperformed *Phragmites* distance (ΔAICc = 0.41), while for reed canary, distance (ΔAICc = 0.00) outperformed reed canary density (ΔAICc = 7.93), thus *Phragmites* density and reed canary distance were retained. At the local (15 m) scale, three models (ΔAICc $\leq$ 2) explained variance in snake occurrence (Table 2.6). Six of eight model parameters retained were associated with probability of snake occurrence. Snake occurrence decreased as canopy cover and distance to shrub increased but increased with increasing vegetation density and distance to invasive reed canary (Table 2.6).

At the exact location scale (1 m x 1 m), significance of model parameters differed between 2-D and 3-D views of habitat variables. The 2-D view had 14 top models with ΔAICc $\leq$ 2 (Table 2.7), while at the 3-D view there were fewer top models (9), but a greater number of model parameters were significantly correlated with probability of snake occurrence (Table 2.8). At the 2-D view, probability of snake occurrence decreased with canopy cover and was greater in the presence of a cover object (Table 2.7). At the 3-D view, canopy cover had a negative effect on snake occurrence, while cover object, % herb, % litter, % coarse woody debris, and % live woody had positive effects (Table 2.8). Sixteen top models with ΔAICc $\leq$ 2 analyzed probability of snake occurrence by vegetation growth form and height (Table 2.9), where shrubs </= 0.46 m and three of four growth forms (shrub, graminoid, forb) at the second height level (> 0.46 to < 1.83 m) had a positive effect on probability of snake occurrence (Table 2.9).

Thermal Habitat

Ground temperature differed amongst habitat types. Of the 10 habitat types, all differed significantly from each other ($H_{(10)} = 13480$, $p < 0.05$ in all cases), except that temperatures in bluff habitat did not differ from those in beach habitat ($p = 0.46$), and temperatures in open sand habitat did not differ from those in old fields ($p = 0.17$; Table 2.10). While ground temperatures of bluff, old field, and beach habitats were the warmest, coniferous, deciduous, and *Phragmites* habitats were the coolest overall (Fig. 2.2). Old field and open sand habitats had the greatest average temperature variation, reaching the highest and lowest temperatures, while coniferous, deciduous, and *Phragmites* habitats had the least temperature variation (Fig. 2.2). Among the invasive grasses, average ground temperature significantly differed by species and whether stands were dead or alive ($H_{(3)} = 1708.2$, $p < 0.05$); *Phragmites* stands were cooler than reed canary (Fig. 2.3; Table 2.11), and live stands were cooler than dead patches (Fig. 2.3; Table 2.11).

Population Demography and Proxies of Individual Fitness

Population demography of Huron County eastern hog-nosed snakes was quantified from 41 different individuals encountered during visual surveys and incidental captures from 2017 to 2020. The greatest number of individuals was encountered in 2018, while the least number of individuals encountered was in 2020 (Table 2.12). While over half of the 41 individuals were PIT-tagged, 2018 was the only year where within-year recaptures occurred (n = 24), and only transmitter-implanted snakes from previous years were recaptured in 2019 (n = 3) and 2020 (n = 3; Table 2.12). Over the four years, all life stages of snakes were observed, with most individuals in the adult or sub-adult age classes (Table 2.13). Over the 2018 - 2020 period, minimum mortality rate was estimated at 31% (Table 2.14). Of the confirmed deceased, 100% of neonate deaths (n = 2) were caused by road mortality, while nearly 60% of adult deaths (n = 4) were caused by predation with the remaining 40% (n = 3) due to human activity (Table 2.14).

For individual fitness proxies, adult body size differed by sex and by population. Compared to Point Pelee (n = 20), eastern hog-nosed snakes from Huron County (n = 17) were larger in both mass (Huron = 424.4 ± 217.0 g, Point Pelee = 307.5 ± 152.4 g; Fig. 2.4) and snout-vent length (SVL; Huron = 721.4 ± 141.5 mm, Point Pelee = 651.1 ± 94.7 mm; Fig. 2.5), but not significantly so (mass: $u_{(35)}$ = 226.5, p = 0.09; SVL; $t_{(35)}$ = 1.75, p = 0.09). Females (Huron: n = 9, Point Pelee: n = 8) were longer (Huron: 820.9 ± 113.4 mm, Point Pelee: 702.4 ± 111.3 mm; Fig. 2.6) and heavier (Huron = 567.7 ± 202.9 g, Point Pelee = 365.0 ± 208.5 g; Fig. 2.7) than males (Huron: n = 8, Point Pelee: n = 12; SVL: Huron = 609.6 ± 63.6 mm, Point Pelee = 616.3 ± 66.5 mm, Fig. 2.6; mass: Huron = 263.1 ± 66.9 g, Point Pelee = 269.2 ± 91.8 g, Fig. 2.7), but the sex differences were significantly only in the Huron population (mass: $u_{(16)}$ = 69, p = 0.002; SVL: $t_{(16)}$ = 4.81, p = 0.0004; Point Pelee mass: $u_{(19)}$ = 63, p = 0.27; SVL: $t_{(19)}$ = 1.95, p = 0.08).

There was a linear positive relationship between log(10) SVL and log(10) body mass (Populations Combined R^2 = 0.91, df = 35; Huron R^2 = 0.93, df = 15; Point Pelee R^2 = 0.87, df = 18). Mean body condition did not differ between populations ($t_{(35)}$ = 1.00, p = 0.32; Fig. 2.8) or between sexes when populations were combined ($t_{(35)}$ = -1.89, p = 0.68) or separately within each population (Huron $t_{(12)}$ = -0.96, p = 0.36; Pelee $t_{(14)}$ = -1.79, p = 0.096; Fig. 2.9). More snakes in Point Pelee had negative residuals compared to snakes in Huron County (Fig. 2.8).

Discussion

Structural and Thermal Habitat

Thermoregulation drives snake habitat selection (Huey et al. 1989; Reinert 1993; Blouin-Demers and Weatherhead 2001a, b, c) and thermal quality is key to habitat suitability (Pringle et al. 2003). One study reported optimal environmental temperatures for eastern hog-nosed snakes ranges between 31 and 34 °C (Texas, USA; Kroll 1973) and although I did not test if ground temperatures differ with structural complexity, complex habitats likely provide thermal refugia when temperatures exceed 34 °C, given their heterogeneity. Vegetation structure can significantly influence ground temperature and yield refugia in the form of structurally complex habitats. For example, shrub cover and open understories are reliable predictors of desert horned lizard (*Phyrnosoma platyrhinos*) occurrence, as shrubs provide significant thermal refuge (e.g., ~20 °C cooler than unshaded bare soils; Newbold and MacMahon 2014) when air temperatures exceed horned lizard maximum voluntary temperature (>39 °C; Brattstrom 1965; Heath 1965; Pianka and Parker 1975). For snake populations that face extreme temperatures, thermal refuge often drives habitat selection (Blouin-Demers and Weatherhead 2001c; Martino et al. 2012; Gardiner et al. 2015; Edkins et al. 2018) and can be critical to surviving thermal extremes. As shrubs and burrows can provide protection from extreme temperatures and temperature fluctuations (Martino et al. 2012; Gardiner et al. 2015; Johnson et al. 2022), the availability and distance to these refugia drives habitat selection in some prairie rattlesnake (*Crotalus viridis*) populations (Gardiner et al. 2015). Structural components can also provide refuge from predators (Shine and Fitzgerald 1996; Pringle et al. 2003; Gardiner et al. 2015). In one study, carpet pythons (*Morelia spilota*) disproportionately used complex treed habitat because dense vine covered within the trees allowed snakes to remain hidden from predators during thermoregulation (Shine and Fitzgerald 1996). As structurally complex habitats readily provide refuge from predators and abiotic threats, some snake species in Ontario also select heterogeneous habitats (Blouin-Demers and Weatherhead 2001c; Hecnar and Hecnar 2011; Maddalena et al. 2020). Amongst coastal dune habitat in Point Pelee National Park, Ontario, woody debris presence, size, and state of decay were important variables in Dekay's brownsnake (*Storeria dekayi*) habitat selection (Hecnar and Hecnar 2011). Woody debris of various sizes and stages of decay created complex habitats and provided brownsnakes with suitable thermal and moisture conditions (Hecnar and Hecnar 2011). In my study, eastern hog-nosed snakes also demonstrated a preference for habitat complexity and the variables associated (positively or negatively) with snake occurrence were related to the availability of cover and thermal suitability. Thus, it appears that habitat selection by Huron County hog-nosed snakes is similar to preferences of other snake species, and selection is likely due to the refuge that habitat complexity provides.

Invasive plants impact critical resources for reptiles. Habitat disturbance restructures vegetation communities (Heisler et al. 2013) and disturbance due to exotic plant introduction alters availability, quality, or distribution of vital resources for herptiles (e.g., food, cover, thermal habitat; Rogalski and Skelly 2012; McDonald and Luck 2013; Cook et al. 2018). As eastern hog-nosed snakes are habitat specialists (require sandy substrates; Platt 1969), I expected a negative association between invasive grass presence and snake occurrence, similarly to other snake habitat specialists. For example, in Wisconsin, USA, Butler's gartersnake (*Thamnophis butleri*) negatively associates with the presence of invasive reed canary grass (*Phalaris arundinacea*; Kapfer et al. 2013). However, my expectation was only partly supported as snake occurrence negatively associated with only one of the grass species. There were very few instances of hog-nosed snakes using *Phragmites* and if used, plant density and height were minimal, yet hog-nosed occurrence was positively associated with reed canary grass, possibly due to the cover it afforded. However, if being taller and denser than neighbouring vegetation drove reed canary use, snakes should have also been positively associated with *Phragmites*.

Phragmites grass can positively or negatively influence resources for herptile, in providing additional food and cover from its detritus (Rogalski and Skelly 2012) or even cause degradation in areas of critical habitat (Markle et al. 2018). As such, it is unclear why snakes did not choose *Phragmites* stands.

Invasive plant presence can influence thermal habitat quality. For snakes, thermoregulatory habitat quality is key to habitat selection and habitat suitability (Huey et al. 1989; Reinert 1993; Blouin-Demers and Weatherhead 2001a, b, c; Pringle et al. 2003). As such, dense stands of invasive plants and their subsequent shade (Randall and Marinelli 1996; Weber 2003; Kaufman and Kaufman 2013) threaten reptile thermal habitat, as shading can degrade thermal quality (Bolton and Brooks 2010; Carter et al. 2015). In some populations optimal environmental temperatures for eastern hog-nosed snakes range between 31 and 34 °C (Kroll 1973) and high quality hog-nosed snake thermal habitat is limited in thermal variation (diurnally and seasonally) and has maximum annual temperatures ranging from 30 to 40 °C (Cunnington 2006). Apart from dead reed canary, neither *Phragmites* or reed canary reached these optimal temperatures, although temperatures of reed canary were significantly warmer and more variable than those of *Phragmites*. *Phragmites* stands also had less variability and consistently cooler temperatures than most other habitat types, while reed canary stands had similar temperatures to other habitat types (e.g., old field). These thermal profile differences are likely driven by maximum height. Differences in maximum height may create climactic buffer discrepancies (McCaughey et al. 1997), as differing vegetation heights impact the amount of sunlight that reaches and warms the ground surface. Exotic plants that grow taller than neighbouring vegetation often provide cooler temperature regimes (Carter et al. 2015). Reed canary can grow to heights between 2 m and 2.8 m (Anderson 2012; Sturtevant et al. 2021), while *Phragmites* grows nearly 8 times taller, reaching heights of up to 15 m (OMNR 2011; Anderson 2012). Thus, substantially taller *Phragmites* inhibits sunlight reaching the ground (Meyerson et al. 2000; Rice et al. 2000), causing cooler surface temperatures than in reed canary stands. As reported in earlier studies (Bolton and Brooks 2010; Cook et al. 2018; Markle et al. 2018), *Phragmites* in Huron County degrades thermal habitat quality for reptiles like eastern hog-nosed snakes. Reed canary, however, appears to be thermally suitable for hog-nosed snakes. While reed canary stands may be relatively cooler than other habitat types, reed canary may serve as refuge during extreme heat events (Oke 1997) or be more thermally suitable than other habitats seasonally (Thomas et al. 1999). While reed canary can grow dense and have ecological impacts (e.g., displace native vegetation), it appears to provide thermally suitable habitat for hog-nosed snakes.

Population Demography and Proxies of Individual Fitness

Anthropogenic activity threatens eastern hog-nosed snake survival. Estimated annual survival rate for Huron County hog-nosed snakes was similar to that in conspecific populations (60%/year for adults; Cunnington 2006; Rouse 2006), yet Huron County had more anthropogenically-induced deaths than most other studies (that reported deaths and causes; Plummer and Mills 2000; Robson 2011; Rouse et al. 2011; Buchanan 2012). Hog-nosed snakes can persist in human modified landscapes, but anthropogenic activity exacerbates existing threats to snake survival (e.g., ~40% of annual adult hog-nosed snake deaths caused by predation; Cunnington 2006; COSEWIC 2007). For example, human activity can subsidize predators by allowing easier access to resources, which cause unnaturally high predator densities (Rosatte 2000; Phillips and Murray 2005). In Wasaga Beach, nearly 40% of adult hog-nosed snake deaths were related to human activity (Cunnington 2004; Featherstone and Anderson 2005), largely conflicts with domesticated dogs (G. Cunnington pers. comm.). Although Huron County does not appear to have higher mortality rates than other populations, there are a suite of threats that challenge snake survival. Road mortality is a well-known threat for many snake species (Row et al. 2007; Fortney et al. 2012; Choquette and Valliant 2016), including some eastern hog-nosed snake populations (Rouse et al. 2011; Robson et al. 2013). During my study none of the radio-tracked snakes died due to road mortality and very few snakes were found dead on the road prior to in-depth monitoring (Huron Stewardship Council 2020). However, scavenging and carcass persistence are known to influence how data from road surveys can accurately represent road mortality rates (Beckmann and Shine 2014). Thus, although I observed relatively low rates of road mortality, my results may not mirror exact rate of road mortality and are only a minimum estimate of hog-nosed snake road mortality in Huron County. Although roads are still dangerous to eastern hog-nosed snakes in Huron County, other competing land-uses pose greater threats to survival. For example, in 2014 a hog-nosed snake resting in an aircraft runway fissure was hit and killed by a runway sweeper (Huron Stewardship Council, unpublished data). In another instance, a radio-tracked individual was killed in 2018 due to a roadside mower (Gallon et al. 2020), while similarly in 2020 another radio-tracked snake was killed in late spring by agricultural activity as heavy machinery had been seeding a crop field. Thus, although human-modified areas can serve as corridors for hog-nosed snakes, using these areas can come with potentially fatal consequences.

Fitness proxies can be used to monitor snakes, and fitness proxies are more informative than presence/absence data and can help determine how well a population persists in the face of human activity. I expected the widespread anthropogenic activity in Huron County to negatively impact snakes such that they would be smaller and in poorer condition. These expectations were not supported, as SVL, body mass, and body condition of snakes in Huron County did not differ significantly from populations in less modified areas near Point Pelee, ON (S. Gillingwater, pers. comm.). Body size and condition of snakes often positively associate with prey availability (Shine and Madsen 1997; Jenkins 2007). I theorize that the noticeably high abundance of preferred prey, American toads (*Anaxyrus americanus*), in the Huron County study area (pers. obs.) may be driving larger body sizes and better body condition of eastern hog-nosed snakes. Although anthropogenic disturbance often impacts reptile fitness, behaviour, body condition, growth, reproduction, and mortality rates (Parent and Weatherhead 2000; Burger 2001; Endriss et al. 2007; Wolf et al. 2013; Lomas et al. 2015; Walkup et al. 2017), snakes can persist in human-modified areas but may demonstrate differences in fitness proxies (Lomas et al. 2015). For example, in a population of northern pacific rattlesnakes (*Crotalus oreganus oreganus*) individuals furthest from human disturbance (>100 m) were heavier and in better condition than individuals close to disturbance (< 100 m; Lomas et al. 2015). Unlike the rattlesnakes however, Huron County eastern hog-nosed snake body size and condition do not appear to be imminently impacted by the modified landscape.

Conclusions

Structurally complex habitats appear to be important for the persistence of eastern hog-nosed snakes in Huron County. Snake movements and habitat selection are often influenced by the thermal quality of habitats (Huey et al. 1989; Webb and Shine 1998; Blouin-Demers and Weatherhead 2001a, b, c). At both localized and exact habitat scales, selection was not random; eastern hog-nosed snakes preferred habitats that offered cover and thermal suitability, as structurally complex habitats create thermal habitat as well as retreats from predators or thermal extremes. Eastern hog-nosed snakes use a variety of habitats (Seburn 2009) and the ability to move between habitat types is critical to population persistence (Seburn 2009). Thus, maintaining the mosaic of complex habitats will be critical to the fitness and persistence of eastern hog-nosed snakes in Huron County.

Ground temperatures of natural habitat types differed from those in invasive grass stands. My study is the first to examine the thermal profile of reed canary grass (*Phalaris arundinacea*) and how invasive reed canary and *Phragmites* grasses influence habitat selection and thermal habitat quality for eastern hog-nosed snakes. Reptiles can be positively (Kapfer et al. 2013; McDonald and Luck 2013) or negatively (Bolton and Brooks 2010; Carter et al. 2015; Cook et al. 2018) influenced by exotic vegetation colonization; I found that eastern hog-nosed snakes demonstrated an aversion to *Phragmites* but a willingness to use reed canary. Thermal profiles suggest that reed canary is suitable for hog-nosed snakes, while cooler temperatures in *Phragmites* stands result in poor quality thermal habitat. While both plant species grow dense and to great heights, maximum height of reed canary is shorter than *Phragmites* and this likely differentiates their thermal qualities. Thus, to preserve critical habitat for hog-nosed snakes, chemical management of *Phragmites* in Huron County should continue. Reed canary appears thermally suitable for hog-nosed snakes, yet it can outcompete native vegetation; therefore, although its management is not critical to enhancing eastern hog-nosed snake habitat, there may be other ecological benefits to managing reed canary grass colonization.

Eastern hog-nosed snakes persist in Huron County's modified landscape, but the population is subject to a unique suite of threats. Aviation infrastructure, agriculture and residential and commercial development all directly threaten Huron County snakes and represent a more diverse suite of threats than those imposed on conspecific populations (Rouse et al. 2011; Robson et al. 2013). Although mortality rate and anthropogenic-induced mortalities were similar to conspecific populations (Plummer and Mills 2000; Robson 2011; Rouse et al. 2011; Buchanan

2012), Huron County individuals were frequently located near anthropogenic activity, regularly encountered near-misses, and experienced human-induced fatalities. While reptiles living in disturbed areas often demonstrate smaller body sizes and poor body condition (Lomas et al. 2015), snakes in Huron County did not appear to be similarly impacted as individuals were larger and in better condition than snakes in conspecific populations in less disturbed areas.

Literature Cited

Adams, B.W., Ehlert, G., Stone, C., Alexander, M., Lawrence, D., Willoughby, M., Moisey, D., Hincz, C., Burkinshaw, A., Richman, J., France, K., DeMaere, C., Kupusch, T., France, T., Broadbent, T., Blonski, L., and Miller, A.J. 2016. Rangeland Health Assessment for Grassland, Forest and Tame Pasture. Alberta Environment & Parks, Rangeland Resource Stewardship Section. iv + 124 pp.

Anderson, H. 2012. Invasive Reed Canary Grass (*Phalaris arundinacea* subsp. *arundinacea*) Best Management Practices in Ontario. Ontario Invasive Plant Council, Peterborough, ON.

Andrews, K.M., Gibbons, J.W., Jochimsen, D.M., and Mitchell, J. 2008. Ecological effects of roads on amphibians and reptiles: a literature review. Herpetological Conservation **3**: 121-143.

Beckmann, C. and Shine, R. 2014. Do the numbers and locations of road-killed anuran carcasses accurately reflect impacts of vehicular traffic? Journal of Wildlife Management **79**: 92-101.

Benson, J.F. and Chamberlain, M.J. 2007. Space use and habitat selection by female Louisiana black bears in the Tensas River Basin of Louisiana. Journal of Wildlife Management **71**(1): 117-126.

Blouin-Demers, G. and Weatherhead, P.J. 2001a. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology **82**: 3025-3043.

Blouin-Demers, G., and Weatherhead, P.J. 2001b. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes *Elaphe obsoleta obsoleta*. Journal of Animal Ecology **70**: 1006-1013.

Blouin-Demers, G. and Weatherhead, P.J. 2001c. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forest. Ecology **82**: 2882-2896.

Blossey B., and McCauley J. 2000. A plan for developing biological control of *Phragmites australis* in North America. Wetland Journal **12**: 23-28.

Bolton, R.M., and Brooks, R.J. 2010. Impact of the seasonal invasion of *Phragmites australis* (Common Reed) on turtle reproductive success. Chelonian Conservation and Biology **9**: 238-243.

Brattstrom, B.H. 1965. Body temperatures of reptiles. American Midland Naturalist **73**: 376-422.

Brown, W.S. 1993. Biology, status and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. Society for the Study of Amphibians and Reptiles, Herpetological Circular **22**: 1-78.

Brown, J.H., Marquet, P.A., and Taper, M.L. 1993. Evolution of body size: consequences of an energetic definition of fitness. The American Naturalist **142**(4): 573-584.

Buchanan, S.W. 2012. Ecology of the eastern hognose snake (*Heterodon platirhinos*) at Cape Cod National Seashore, Barnstable County, Massachusetts. M.Sc. Thesis, Biology, Montclair State University, Montclair, New Jersey.

Buchanan, S.W., Timm, B.C., Cook, R.P., Couse, R., and Hazard, L.C. 2017. Spatial ecology and habitat selection of eastern hognose snakes. Journal of Wildlife Management **81**(3): 509-520.

Burger, J. 2001. The behavioral response of basking Northern water (*Nerodia sipedon*) and Eastern garter (*Thamnophis sirtalis*) snakes to pedestrians in a New Jersey park. Urban Ecosystems **5**(2): 119-129.

Burnham, K.P., and Anderson, D.R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. 2nd Edition, Springer-Verlag, New York, NY, USA

Carter, E.T., Eads, B.C., Ravesi, M.J., and Kingsbury, B.A. 2015. Exotic invasive plants alter thermal regimes: implications for management using a case study of a native ectotherm. Functional Ecology **29**: 683-693.

Casper, G.S., Anton, T.G., Hay, R.W., Holycross, A.T., King, R.S., Kingsbury, B.A., Mauger, D., Parent, C., Phillips, C.A., Resetar, A., Seigel, R.A., and Wilson, T.P. 2001. Recommended standard survey protocol for the Eastern Massasauga, *Sisturus catenatus catenatus*. US Fish and Wildlife Service, Fort Snelling, MN. 9 pp.

Choquette, J.D., and Valliant, L. 2016. Road mortality of reptiles and other wildlife at the Ojibway Prairie Complex and greater park ecosystem in southern Ontario. Canadian Field Naturalist **130**: 64-75.

CNES (Centre National d'Etudes Spatiales). 2020. Aerial Imagery. Centre National d'Etudes Spatiales, Paris, France.

Compton, B.W., Rhymer, J.M., and McCollough, M. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): An application of paired logistic regression. *Ecology* **83**(3): 833-843.

Cook, C.E, McCluskey, A.M, Chambers, R.M. 2018. Impacts of invasive *Phragmites australis* on diamondback terrapin nesting in Chesapeake Bay. Estuaries and Coasts **41**: 966-973.

COSEWIC. 2007. COSEWIC Assessment and Update Status Report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. viii + 36 pp.

COSEWIC. 2019. Committee on the Status of Endangered Wildlife in Canada. Available from: http://www.cosewic.ca/index.php/en-ca/ [Accessed 20 November 2019].

COSEWIC. 2021. COSEWIC Assessment and Update Status Report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xi + 45 pp.

Crawshaw, G., and Lentini, A. 2013. Invasive Procedures Protocol for Snakes. Prepared for the Animal Care Committee.

Cummings, F.H., Morris, K., and McLennan, D. 1998. Economic Impact of Agriculture on the Economy of Huron County. School of Rural Planning and Development. University of Guelph, Guelph, ON. pp. 1-58.

Cunnington, G. 2004. Modelling habitat use by eastern hog-nosed snakes (*Heterodon platirhinos*) in Wasaga Beach Provincial Park, Ontario. Undergraduate thesis, Trent University, Peterborough, Ontario.

Cunnington, G.M. and Cebek, J.E. 2005. Mating and nesting behavior of the eastern hognose snake (*Heterodon platirhinos*) in the northern portion of its range. American Midland Naturalist **154**(2): 474-478.

Cunnington, G.M. 2006. Biotic and abiotic variables that alter ground surface temperature and habitat quality for eastern hog-nosed snakes (*Heterodon platirhinos*). M.Sc. Thesis, Watershed Ecosystem Graduate Program, Peterborough, Ontario.

Diller, L.V. and Wallace, R.L. 1984. Reproductive biology of the northern pacific rattlesnake (*Crotalus viridis oreganus*) in Idaho. Herpetologica **40**: 182-193.

Eastern Massasauga Recovery Team (EMRT). 2005. Guidelines for identifying significant habitat, and significant wildlife habitat, for the Massasauga in Eastern Georgian Bay and Bruce Peninsula Populations, Ontario. Version 1.0.

Edkins, T.L., Somers, C.M., Vanderwel, M.C., Sadar, M.J., and Poulin, R.G. 2018. Variable habitat selection and movement patterns among Bullsnake (*Pituophis catenifer sayi*) populations in Saskatchewan. Canadian Field-Naturalist **132**(2): 126-139.

Endriss, D.A., Hellgre, E.C., Fox, S.F., and Moody, R.W. 2007. Demography of an urban population of the Texas horned lizard (*Phyrnosoma cornutum*) in central Oklahoma. Herpetologica **63**(3): 320-331.

ESRI. 2021. ArcMap 10.5.1. Environmental Systems Research Institute, Redlands, California.

Ettling, J.A., Aghasyan, L.A., Aghasyan, A.L., and Parker, P.G. 2013. Spatial ecology of Armenian vipers, *Montivipera raddei*, in a human-modified landscape. Copeia **2013**: 64-71.

Featherstone, D. and Anderson, S. 2005. Eastern Hog-nosed Snake Discussion Paper. Prepared for Nottawasaga Valley Conservation Authority, Wasaga Beach, ON. viii + 24 pp.

Fortney, A.N., Poulin, R.G., Martino, J.A., Parker, D.L., and Somers, C.M. 2012. Proximity to hibernacula and road type influence potential road mortality of snakes in southwestern Saskatchewan. Canadian Field-Naturalist **126**(3): 194-203.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology **10**: 1500-1508.

Gallon, A., Maddalena, M. and Watt, C. 2020. Eastern Hog-nosed Snake Conservation in Huron County: Final 2019/2020 Report. Unpublished report to Ontario Ministry of Natural Resources and Forestry. Huron Stewardship Council. Huron County, ON. i + 20 pp.

Gardiner, L.E., Somers, C.M., Parker, D.L., and Poulin, R.G. 2015. Microhabitat selection by prairie rattlesnakes (*Crotalus viridis*) at the northern extreme of their geographic range. Journal of Herpetology **49**(1): 131-137.

Goulet, C., Litvaitis, J., and Marchand, M.N. 2015. Habitat associations of the eastern hognose snake at the northern edge of its geographic distribution: should a remnant population guide restoration? Northeastern Naturalist **22**: 530-540.

Hansen, N.A., Sato, C.F., Michael, D.R., Lindenmayer, D.B., and Driscoll, D.A. 2019. Predation risk for reptiles is highest at remnant edges in agricultural landscapes. Journal of Applied Ecology **56**: 31-43.

Harding, J.H. 1997. Amphibians and Reptiles of the Great Lakes Region. University of Michigan Press, Ann Arbor, MI. 378 pp.

Harvey, D.S. 2008. Massasauga monitoring—analysis and recommendations v.1.2. Report submitted to the Bruce Peninsula National Park / Fathom Five National Marine Park, Parks Canada Agency, Ontario.

Heath, J.E. 1965. Temperature regulation and diurnal activity in horned lizards. University of California Publications in Zoology **64**: 97-136.

Hecnar, S.J. 1997. Amphibian Pond Communities in Southwestern Ontario. *In* Amphibians In Decline: Canadian Studies of Global Phenomenon, D.M. Green (ed.). Herpetological Conservation **1**: 1-15.

Hecnar, S.J. and Hecnar, D.R. 2011. Selection of woody debris by Dekay's brownsnake (*Storeria dekayi*) in a dune habitat in Ontario, Canada. Journal of Herpetology **45**(4): 478-483.

Heisler, L.M., Somers, C.M., Wellicome, T.I., and Poulin, R.G. 2013 Landscape-scale features affecting small mammal assemblages on the northern Great Plains of North America. Journal of Mammalogy **94**(5): 1059-1067.

Hoffman, D.W., Richards, N.R., and Morwick, F.F. 1952. Soil Survey of Huron County. Ontario Soil Survey Rep. No. 13, Experimental Farms Service, Canada Department of Agriculture, and Ontario Agricultural College, Guelph, ON.

Huey, R.B., Peterson, C.R., Arnold, S.J. and Porter, W. 1989. Hot rocks and not-so-hot rocks: retreat site selection by garter snake and its thermal consequences. Ecology **70**: 931-934.

Huron Stewardship Council. 2020. Species at Risk Stewardship Fund Interim Progress Report. Unpublished report for Ontario Ministry of Natural Resources and Forestry. 4 pp.

Hurvich, C.M., and Tsai, C. 1989. Regression and time series model selection in small samples. Biometrika **76**(2): 297-307.

Iglesias-Carrasco, M., Head, M.L., Jennions, M.D., and Cabido, C. 2016. Condition-dependent trade offs between sexual traits, body condition and immunity: the effect of novel habitats. BMC Evolutionary Biology **16**(1): 135-144. doi: 10.1186/s12862-016-0706-0.

Jenkins, C.L. 2007. Ecology and conservation of rattlesnakes in sagebrush steppe ecosystems: Landscape disturbance, small mammal communities, and Great Basin rattlesnake reproduction. Ph.D. thesis, Biology, Idaho State University, Pocatello, Idaho.

Jenkins, C.L., Peterson, C.R., Doering, S.C., and Cobb, V.A. 2009. Microgeographic characteristics among Western Rattlesnake (*Crotalus oreganus*) populations. Copeia **2009**: 774-780.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, **61**(1): 65-71.

Johnson, N.B., Poulin, R.G., and Somers, C.M. 2022. Thermoregulation by bullsnakes (*Pituophis catenifer sayi*): do burrows make life easier on the prairies? Canadian Journal of Zoology: **100**(5): 303-314.

Kapfer, J.M., Doehler, K., and Hay, R. 2013. The influence of habitat type and the presence of an invasive wetland plant (*Phalaris arundinacea*) on capture rates of sympatric rare and common gartersnake species (*Thamnophis butleri* and *Thamnophis sirtalis*). Journal of Herpetology **47**(1): 126-130.

Kaufman, S.R., and Kaufman, W. 2013. Invasive Plants: A Guide to Identification, Impacts, and Control of Common North American Species. Stackpole Books, Mechanicsburg, PA. 464p.

Kerr, J.T. and Cihlar, J. 2003. Land use and cover with intensity of agriculture for Canada from satellite and census data. Global Ecology and Biogeography **12**(6): 161-172.

King County. 2010. Noxious Weed Control Program: Common Reed – Phragmites Best Management Practices. King County, WA, USA. Available from: https://your.kingcounty.gov/dnrp/library/water-and-land/weeds/BMPs/common-reed-phragmites-control.pdf [Accessed 12 May 2019].

Kraus, T. 2011. Recovery Strategy for the Eastern Hog-nosed Snake (*Heterodon platirhinos*) in Ontario. Ontario Recovery Strategy Series. Prepared for the Ontario Ministry of Natural Resources, Peterborough, Ontario. i + 6 pp. + Appendix vi + 24 pp. Adoption of the Recovery Strategy for the Eastern Hog-nosed Snake (*Heterodon platirhinos*) in Canada (Seburn, 2009).

Kroll, J.C. 1973. Comparative physiological ecology of eastern and western hognose snakes (*Heterodon platirhinos* and *Heterodon nasicus*). PhD. thesis, Texas A&M University, College Station, Texas. 261 pp.

Lagory, K.E., Walston, L.J., Goulet, C., Van Lonkhuyzen, R.A., Najjar, S., and Andrews, C. 2009. An examination of scale-dependent resource use by eastern hognose snakes in Southcentral New Hampshire. Journal of Wildlife Management **78**(3): 1387-1393.

Lake Huron Centre for Coastal Conservation (LHCCC) 2019. Programs: Brucedale Phragmites Management. https://www.lakehuron.ca/brucedale [Accessed 27 November 2019].

Lawton, J.H. 1993. Range, population abundance and conservation. Trends in Ecology and Evolution **8**: 409-413.

Lelièvre, H.G., Blouin-Demers, G., Bonnet, X., and Lourdais, O. 2010. Thermal benefits of artificial shelters in snakes: A radiotelemetric study of two sympatric colubrids. Journal of Thermal Biology **35**: 324-331.

Lelièvre, H.G., Blouin-Demers, G., Pinaud, D., Lisse, H., Bonnet, X., and Lourdais, O. 2011. Contrasted thermal preferences translate into divergences in habitat use and realized performance in two sympatric snakes. Journal of Zoology **284**: 265-275.

Lesbarrères, D., Ashpole, S.L., Bishop, C.A., Blouin-Demers, G., Brooks, R.J., Echaubard, P., Govindarajulu, P., Green, D.M., Hecnar, S.J., Herman, T., Houlahan, J., Litzgus, J.D., Mazerolle, M.J., Paszkowski, C.A., Rutherford, P., Schock, D.M., Storey, K.B., and Lougheed, S.C. 2014. Conservation of herpetofauna in northern landscapes: threats and challenges from a Canadian perspective. Biological Conservation **170**: 48-55.

Lesica, P. and Allendorf, F.W. 1995. When are peripheral populations valuable for conservation? Conservation Biology **9**(4): 753-760.

Leuenberger, W. Davis, A.G., McKenzie, J.M., Drayer, A.N., and Price, S.J. 2019. Snake density using passive integrated transponder (PIT) telemetry and spatial capture-recapture analyses for linear habitats. Journal of Herpetology **4**: 272-281.

Levin, D.A. 1970. Developmental instability and evolution in peripheral isolates. American Naturalist **104**: 343-353.

Litzgus, J.D., and Brooks, R.J. 1998. Reproduction in a northern population of *Clemmys guttata*. Journal of Herpetology **32**: 252-259.

Litzgus, J.D., F. Bolton, and A.I. Schulte-Hostedde. 2008. Reproductive output depends on body condition in spotted turtles (*Clemmys guttata*). Copeia **2008**(1): 84-90.

Lomas, E., Larsen, K.W., and Bishop, C.A. 2015. Persistence of northern pacific rattlesnakes masks the impact of human disturbance on weight and body condition. Animal Conservation **18**: 548-556.

Maddalena, M.P., Row, J.R., Dyson, M.E., Blouin-Demers, G., and Fedy, B.C. 2020. Movement and habitat selection of eastern milksnakes (*Lampropeltis triangulum*) at intact and fragmented sites. Copeia **108**(4): 847-854.

Manly, B.F. J., McDonald, L.L., Thomas, D.L., McDonald, T.L., and Erickson, W.P. 2002. Resource selection by animals: statistical design and analysis of field studies. Kluwar Academic Publishers, Dordrecht, The Netherlands. pp. 29.

Markle, C.E., Chow-Fraser, G., and Chow-Fraser, P. 2018. Long-term habitat changes in a protected area: Implications for herpetofauna habitat management and restoration. PLoS ONE **13**(2): 1-15.

Matlack, G.R. 1993. Microenvironment variation within and among forest edge sites in the eastern United-States. Biological Conservation **66**: 185-194.

Martino, J.A., Poulin, R.G., Parker, D.L., and Somers, C.M. 2012. Habitat selection by grassland snakes at northern range limits: implications for conservation. Journal of Wildlife Management **76**(4): 759-767.
Martin, L.J. and Blossey, B. 2013. The runaway weed: costs and failures of *Phrasgmites australis* management in the USA. Estuaries and Coasts **36**: 626-632.
Mccardle, L.D., and Fontenot, C.L. 2016. The influence of thermal biology on road mortality risk in snakes. Journal of Thermal Biology **56**: 39-49.
McCaughey, J.H., Amiro, B.D., Robertson, A.W., and Spittlehouse, D.L. 1997. Forest Environments. *In* The Surface Climates of Canada, W.G. Bailey, T.R., Oke, and W.R. Rouse (Eds.). Montreal and Kingston, ON McGill-Queens' University Press.
McDonald, P., and Luck G. 2013. Density of an environmental weed predicts the occurrence of the king brown snake (*Pseudechis australis*) in central Australia. Herpetological Journal **23**(3): 161-165.
Meyerson, L.A., Saltonstall, K, Windham, L., Kiviat, E., Findlay, S. 2000. A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. Wetlands Ecology and Management **8**: 89-103.
Moore, M.J.C., and Seigel, R.A. 2006. No place to nest or bask: Effects of human disturbance on the nesting and basking habits of yellow-blotched map turtles (*Graptemys flavimaculata*). Biological Conservation **130**: 386-393.
Mullin, S.J., and Seigel, R.A., editors. 2009. Snakes: Ecology and Conservation. Cornell University Press, Ithaca, New York, USA.
Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology & Evolution **10**: 58-62.
Naulleau, G., and Bonnet, X. 1996. Body condition threshold for breeding in a viviparous snake. Oecologica **107**: 301-306.
Newbold, T.A.S., and MacMahon, J.A. 2014. Determinants of habitat selection by desert horned lizards (*Phyrnosoma platyrhinos*): The importance of abiotic factors associated with vegetation structure. Journal of Herpetology **48**(3): 306-316.
OFAH/OMNRF Invading Species Awareness Program. 2012. Invasive Phragmites. Available from: http://www.invadingspecies.com/invasive-phragmites/ [Accessed 14 March 2019].
OIPC. 2019. Ontario Invasive Phragmites Working Group: Phragmites-Native vs. Invasive. Available from: https://www.opwg.ca/phragmites/native-vs-invasive/ [Accessed 19 August 2019].
Oke, T.R. 1997. Surface Climate Processes. *In:* The Surface Climates of Canada, Bailey, W.G., Oke, T.R., and Rouse, W.R. (eds.). Montreal and Kingston, ON: McGill-Queens' University Press.
OMNR. 2011. Invasive *Phragmites*—Best Management Practices. Ontario Ministry of Natural Resources. Peterborough, ON. Version 2011. 15pp.
OMNRF. 2016a. Eastern Hog-nosed Snake Government Response Statement. Ontario Ministry of Natural Resources and Forestry, Species Conservation Policy Branch. Peterborough, ON. 6 pp.
OMNRF. 2016b. Survey Protocol for Ontario's Species at Risk Snakes. Ontario Ministry of Natural Resources and Forestry, Species Conservation Policy Branch. Peterborough, ON. ii + 17 pp.

OMNRF. 2018. The Ecosystems of Ontario—Part 1: Ecozones and Ecoregions. Available from: https://www.ontario.ca/page/ecosystems-ontario-part-1-ecozones-and-ecoregions [Accessed 27 November 2019].

Parent, C., and Weatherhead, P. J. 2000. Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. Oecologia **125**(2): 170-178.

Peet-Paré, C.A., and Blouin-Demers, G. 2012. Female eastern hog-nosed snakes (*Heterodon platirhinos*) choose nest sites that produce offspring with phenotypes likely to improve fitness. Canadian Journal of Zoology **90**: 1215-1230.

Pianka, E.R., and Parker, W.S. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. Copeia **1975**: 141-162.

Picard, G., Carrière, M., Blouin-Demers, G. 2011. Common musk turtles (*Sternotherus odoratus*) select habitats of high thermal quality at the northern extreme of their range. Amphibia-Reptilia **32**: 83-92.

Phillips, J. and Murray, D. 2005. Raccoon (*Procyon lotor*) population demographics in Point Pelee National Park and implications for the management of turtle species at risk. Unpublished report to Point Pelee National Park, Parks Canada. 49 pp.

Platt, D.R. 1969. Natural history of the hognose snake *Heterodon platyrhinos* and *Heterodon nasicus*. University of Kansas Publications, Museum of Natural History **18**(4): 253-420.

Plummer, M.V., and Mills, N.E. 2000. Spatial ecology and survivorship of resident and translocated hognose snakes (*Heterodon platirhinos*). Journal of Herpetology **34**(4): 565-575.

Pringle, R.M., Webb, J.K., and Shine, R. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. Ecology **84**: 2668-2679.

Putman, B.J., Gasca, M., Blumstein, D.T., and Pauly, G.B. 2019. Downsizing for downtown: limb lengths, toe lengths, and scale counts decrease with urbanization in western fence lizards (*Sceloporous occidentalis*). Urban Ecosystems **22**: 1071-1081.

Quirion, B., Simek, Z., Dávalos, A., and Blossey, B. 2018. Management of invasive *Phragmites australis* in the Adirondacks: a cautionary tale about prospects of eradication. Biological Invasions **20**: 59-73.

Randall, J.M., and Martinelli, J. 1996. Invasive Plants: Weeds of the Global Garden. Brooklyn Botanical Garden, Brooklyn, NY. 112 pp.

Reading, C. 2004. The influence of body condition and prey availability on female breeding success in the smooth snake (*Coronella austriaca* Laurenti). Journal of Zoology **264**: 61-67.

Reinert, H.K. 1993. Habitat selection in snakes. *In* Snakes: Ecology and Behaviour. *Edited by* R.A. Seigel & J.T. Collins, The Blackburn Press, Caldwell. pp. 201-240.

Rice, D., Rooth, J., and Court Stevenson, J. 2000. Colonization and expansion of *Phragmites australis* in upper Chesapeake Bay tidal marshes. Wetlands **20**: 280-299.

Robson, L.E. 2011. The spatial ecology of eastern hognose snakes *(Heterodon platirhinos*): habitat selection, home range size, and the effect of roads on movement patterns. M.Sc. thesis, Biology, University of Ottawa, Ottawa, Ontario.

Robson, L.E., and Blouin-Demers, G. 2013. Eastern hognose snakes (*Heterodon platirhinos*) avoid crossing paved roads, but not unpaved roads. Copeia **3**: 507-511.

Rogalski, M.A., Skelly, D.K. 2012. Positive effects of nonnative invasive *Phragmites australis* on larval bullfrogs. PLOS One **7**(8): 1-8.

Rosatte, R.C. 2000. Management of raccoons (*Procyon lotor*) in Ontario, Canada: do human intervention and disease have significant impact on raccoon populations? Mammalia **64**: 369-390.
Rouse, J. 2006. Spatial ecology of the eastern massasauga (*Sisturus catenatus*) and the eastern hog-nosed snake (*Heterodon platirhinos*) in a rock-barren landscape. M.Sc. thesis. University of Guelph, Guelph, Ontario.
Rouse, J.D., Wilson, R.J., Black, R., and Brooks, R.J. 2011. Movement and spatial dispersion of *Sisturus catenatus* and *Heterodon platirhinos*: Implications for interactions with roads. Copeia **2011**(3): 443-456.
Row, J.R. and Blouin-Demers, G. 2006a. Thermal quality influences effectiveness of thermoregulation, habitat use, and behaviour in milk snakes. Oecologia **148**: 1-11.
Row, J.R. and Blouin-Demers, G. 2006b. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. Ecoscience **13**(4): 443-450.
Row, J.R., Blouin-Demers, G., and Weatherhead, P. 2007. Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). Biological Conservation **137**(1): 117-124.
Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., and Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. Science **287**: 1770-1774.
Saltonstall, K. and Hauber, D. 2007. Notes on *Phragmites australis* (Poacease: Arundinoideae) in North America. Journal of the Botanical Research Institute of Texas **1**(1): 385-388.
Seburn, D. 2009. Recovery Strategy for the Eastern Hog-nosed Snake (*Heterodon platirhinos*) in Canada. *Species at Risk Act* Recovery Strategy Series. Parks Canada Agency, Ottawa, ON, 24 pp.
Shine, R., and Fitzgerald, M. 1996. Large snakes in a mosaic rural landscape: the ecology of carpet pythons *Morelia spilota* (Serpentes: Pythonidae) in coastal eastern Australia. Biological Conservation **76**: 113-122.
Shine, R. and Madsen, T. 1997. Prey abundance and predator reproduction: rats and pythons on a tropical Australian floodplain. Ecology **78**(4): 1078-1086.
Shoemaker, K.T., and Gibbs, J.P. 2010. Evaluating basking-habitat deficiency in the threatened eastern massasauga rattlesnake. Journal of Wildlife Management **74**: 504-513.
Somers, C.M., Neudorf, K., Jones, K.L. and Lance, S.L. 2011. Novel microsatellite loci for the compost earthworm *Eisenia fetida*: A genetic comparison of three North American vermiculture stocks. Pedobiologia **54**: 111-117.
Statutes of Canada. 2002. Species at Risk Act, c. 29. https://laws.justice.gc.ca/eng/acts/s-15.3
Sturtevant, R., Dettloff, K., and Conard, W. 2021. *Phalaris arundinacea* L.: U.S. Geological Survey, Nonindigenous Species Information System, Gainesville, FL, and NOAA Great Lakes Aquatic Nonindigenous Species Information System, Ann Arbor, MI. Available from: https://nas.er.usgs.gov/queries/greatlakes/FactSheet.aspx?SpeciesID=2938 [Accessed 24 April 2021].
Therneau, T. 2022. survival: A Package for Survival Analysis in R. R package version 3.3-1.
Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D., and Webb, N.R. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. Functional Ecology **13**: 55-64.

Vanek, J.P., and Wasko, D.K. 2017. Spatial ecology of the eastern hog-nosed snake (*Heterodon platirhinos*) at the northeastern limit of its range. Herpetological Conservation and Biology **12**: 109-118.

Walkup, D.K., Leavitt, D.J., and Fitzgerald, L.A. 2017. Effects of habitat fragmentation on population structure of dune-dwelling lizards. Ecosphere **8**(3): 1-14.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O., and Bairlein, F. 2002. Ecological responses to recent climate change. Nature **416**: 389-395.

Weatherhead, P. J., and Brown, G. P. 1996. Measurement versus estimation of condition in snakes. Canadian Journal of Zoology **74**: 1617-1621.

Webb, J.K., and Shine, R. 1998. Thermoregulation by a nocturnal elapid snake (*Hoplocephalus bungaroides*) in south-eastern Australia. Physiological Zoology **71**: 680-692.

Weber, E. 2003. Invasive Plant Species of the World: A Reference Guide to Environmental Weeds. CAB International Publishing, Wallingford, UK. viii + 548 pp.

Weinstein, M.P. and Balletro, J.H. 1999. Does the common reed, *Phragmites australis*, affect essential fish habitat? Estuaries **22**: 793-802.

Wilder, S.M., Raubenheimer, D., and Simpson, S.J. 2016. Moving beyond body condition indices as an estimate of fitness in ecological and evolutionary studies. Functional Ecology **30**: 108-115.

Wilson, R. 2004. Invasive Procedures Protocol for Snakes. Prepared for the Snake and Lizard Advisory Group.

Wolf, A.J., Hellgren, E.C., III Bogosian, V., and Moody, R.W. 2013. Effects of habitat disturbance on Texas horned lizards: an urban case study. Herpetologica **69**(3): 265-281.

Appendix 2A

Table 2.1. Variables used to characterize eastern hog-nosed snake (*Heterodon platirhinos*) habitat in Huron County, ON at the local scale (within 15 m radius of snake telemetry location). Habitat surveys were completed within 14 days of determining snake radio locations and were completed as paired 'used'-'available' plot surveys where available habitat was represented by plots determined by randomly generated bearings (1 - 360°) and number of steps (1 - 50 steps).

Potential Variables of the Localized Habitat Model (15 m)	
Canopy	Average overhead canopy (%) measured in 4 cardinal directions using a densiometer.
Distance to Cover	Distance to nearest object large enough to conceal an adult snake, within 15 m.
Distance to Edge	Distance to forest edge (adjoining canopy of >10 trees with DBH >7.5 cm) within 15 m.
Distance to Shrub	Distance to closest single shrub (>50 cm in height) or >10 clumped shrub seedlings (<50 cm in height), large enough to conceal an adult snake within 15 m.
Distance to Tree	Distance to closest tree (DBH >7.5 cm; Peet-Paré & Blouin-Demers 2012) within 15 m.
Distance to Reed	Distance to Reed Canary grass within 15 m.
Distance to Phrag	Distance to Phragmites grass within 15 m.
Reed Density	Density of Reed Canary grass plants and patches within 15 m.
Phrag Density	Density of Phragmites grass plants and patches within 15 m.
Veg Density	Average height and density of vegetation in 4 cardinal directions, measured with a Robel pole to determine maximums and minimums.

Table 2.2. Variables used to characterize eastern hog-nosed snake (*Heterodon platirhinos*) habitat in Huron County, ON at the exact location scale (within a 1 x 1 m quadrat centred on snake telemetry location). Habitat surveys were completed within 14 days of determining snake radio locations and were completed as paired 'used'-'available' plot surveys where available habitat was represented by plots determined by randomly generated bearings (1 - 360°) and number of steps (1 - 50 steps).

Potential Variables of the Exact Location Model (within a 1 x 1 m plot)	
Canopy	Average overhead canopy (%) measured in 4 cardinal directions using a densiometer.
Cover Presence	Whether a cover object large enough to conceal an adult snake is present.
% Live Woody	Percent live woody vegetation cover within plot.
% CWD	Percent coarse woody debris (CWD) cover within plot.
% Herb	Percent herbaceous vegetation cover within plot.
% Litter	Percent herbaceous litter within plot.
% Ground	Percent bare ground within plot.
% Tree	Percent cover by tree species within plot.
% Shrub	Percent cover by shrub species within plot.
% Forb	Percent cover by broad-leaved herbaceous plants within the plot.
% Graminoid	Percent graminoid plants present within the plot.
Reed Cover	Percent cover by Reed Canary grass within plot.
Phrag Cover	Percent cover by Phragmites grass within plot.
Veg Density	Average height and density of vegetation in 4 cardinal directions, measured with a Robel pole to determine maximums and minimums.

Table 2.3. Vegetation variables by life form and height (Alberta Riparian Habitat Management Society 2008) at the exact location scale (within 1 x 1 m quadrat centred on snake telemetry location) available for use by eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County, ON.

Potential Variables of the Growth & Height Model (within a 1 x 1 m plot)	
oneTree	Cover (%) by tree species 0 to <0.46 m tall within the plot.
oneShrub	Cover (%) by shrub species 0 to <0.46 m tall within the plot.
oneGram	Cover (%) by graminoid species 0 to <0.46 m tall within the plot.
oneForb	Cover (%) by forb species 0 to <0.46 m tall within the plot.
twoTree	Cover (%) by tree species >0.46 to <1.83 m tall within the plot.
twoShrub	Cover (%) by shrub species >0.46 to <1.83 m tall within the plot.
twoGram	Cover (%) by graminoid species >0.46 to <1.83 m tall within the plot.
twoForb	Cover (%) by forb species >0.46 to <1.83 m tall within the plot.
threeTree	Cover (%) by tree species >1.83 m within the plot.
threeShrub	Cover (%) by shrub species >1.83 m within the plot.
threeGram	Cover (%) by graminoid species >1.83 m within the plot.
threeForb	Cover (%) by forb species >1.83 m within the plot.

Table 2.4. Invasive plant distribution and density classes (Adams et al. 2016) referenced to record presence of *Phragmites a. australis* and *Phalaris arundinacea* patches within eastern hog-nosed snake (*Heterodon platirhinos*) habitat in Huron County, ON at the local scale (within a 15 m radius of snake radio locations).

Class	Description of abundance in polygon	Distribution
0	None	
1	Rare	
2	A few sporadically occurring individual plants	
3	A single patch	
4	A single patch plus a few sporadically occurring plants	
5	Several sporadically occurring plants	
6	A single patch plus several sporadically occurring plants	
7	A few patches	
8	A few patches plus several sporadically occurring plants	
9	Several well spaced patches	
10	Continuous uniform occurrences of well spaced plants	
11	Continuous occurrence of plants with a few gaps in the distribution	
12	Continuous dense occurrence of plants	
13	Continuous occurrence of plants with a distinct linear edge in the polygon	

Table 2.5. Habitat types available to eastern hog-nosed snakes (*Heterodon platirhinos*) in the Huron County, ON study area located in the mixed-woods plains ecozone (OMNRF 2018).

Habitat Type	**Description**
Beach	Sand dune and dune grass dominant, along shoreline of Great Lake
Deciduous Forest	Deciduous tree species dominant forest
Coniferous Forest	Coniferous tree species dominant forest
Large River Riparian Area	Within proximity of large river system, characterized by flooding and soil saturation; cobblestones a co-dominant substrate for the riparian and disturbance-based vegetation communities
Sparsely Vegetated Bluff-side	Eroding bluff-side with predominantly clay substrate, lacking deep binding root mass
Old Field	Once cleared for agriculture, area now fallow and revegetating with a disturbed vegetation community (ie. dominated by at least 50% non-native species and re-establishing native species)
Open-canopy *Juniperus* Shrubland	Absent upper canopy, *Juniperus* shrub and sandy substrate dominant
Live RC	Patch of live reed canary grass (*Phalaris arundinacea)*
Live PH	Patch of live *Phragmites* (*Phragmites a. australis)*
Dead RC	Patch of standing dead reed canary grass (*Phalaris arundinacea)*
Dead PH	Patch of standing dead *Phragmites* (*Phragmites a. australis)*

Table 2.6. Resource selection function assessing local (within 15 m) habitat variables predicting eastern hog-nosed snake (*Heterodon platirhinos*) occurrence in Huron County, ON. A total of 512 models were fit for all possible predictor combinations, with only the null model and top models with ΔAICc ≤ 2 shown. The Akaike's Information Criterion value (AICc) difference from top model in AIC score (ΔAICc), Akaike weights, and number of parameters (K) of the models are included. Estimates, standard errors (SE), ΔAICc, and Akaike weights are presented for model parameters.

Localized Habitat Model (within 15 m) Formula	**K**	**AICc**	**ΔAICc**	**Weight**
Occurrence ~ Intercept	0	227.35	25.30	4.27E-07
Occurrence ~ Canopy + Distance to Shrub + Distance to Reed + Veg Density	4	202.10	0.00	0.13
Occurrence ~ Canopy + Distance to Cover + Distance to Shrub + Distance to Reed + Veg Density	5	202.15	0.10	0.13
Occurrence ~ Canopy + Distance to Shrub + Distance to Tree + Distance to Reed + Veg Density	5	204.03	1.98	0.05

Top Model Variables (within 15 m)

Parameter	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Canopy	-0.71	0.31	-1.21	-0.20
Distance to Tree	0.06	0.27	-0.39	0.50
Distance to Shrub	-0.45	0.22	-0.82	-0.09
Distance to Cover	-0.29	0.24	-0.68	0.11
Distance to Reed	0.77	0.36	0.18	1.36
Veg Density	0.64	0.21	0.30	0.98

Table 2.7. Resource selection function assessing habitat variables at the exact location scale (1 x 1 m) from a 2-D view as predictors of eastern hog-nosed snake (*Heterodon platirhinos*) occurrence in Huron County, ON. A total of 2048 models were fit for all possible predictor combinations, with only null and top models with ΔAICc ≤ 2 shown. The Akaike's Information Criterion value (AICc) difference from top model in AIC score (ΔAICc), Akaike weights, and number of parameters (K) of the models are included. Estimates, standard errors (SE), ΔAICc, and Akaike weights are presented for model parameters.

Exact Location Model (1 x 1 m) Formula - 2D	K	AIC	ΔAIC	Weight
Occurrence ~ Intercept	**0**	**227.35**	**46.03**	**3.11E-12**
Occurrence ~ Canopy + Cover Presence + % Ground + % Litter	4	181.32	0.00	0.03
Occurrence ~ Canopy + Cover Presence + % Ground + % Litter + Veg Density	5	181.78	0.46	0.02
Occurrence ~ Canopy + Cover Presence + % Ground + Veg Density	4	181.87	0.55	0.02
Occurrence ~ Canopy + Cover Presence + % Ground + % Live Woody	4	182.02	0.70	0.02
Occurrence ~ Canopy + Cover Presence + % Ground	3	182.12	0.80	0.02
Occurrence ~ Canopy + Cover Presence + % Ground + % Litter + % Herb	5	182.44	1.12	0.02
Occurrence ~ Canopy + Cover Presence + % Ground + % Litter + % Live Woody	5	182.47	1.15	0.02
Occurrence ~ Canopy + Cover Presence + % Ground + % Litter + Reed Cover	5	182.73	1.41	0.02
Occurrence ~ Canopy + Cover Presence + % Ground + Reed Cover + Veg Density	5	182.79	1.47	0.02
Occurrence ~ Cover Presence + % Ground + % Litter	3	182.80	1.48	0.01
Occurrence ~ Canopy + Cover Presence + % Ground + % Litter + Reed Cover + Veg Density	6	182.80	1.48	0.01
Occurrence ~ Canopy + Cover Presence + % CWD + % Ground + % Live Woody	5	182.88	1.56	0.01
Occurrence ~ Canopy + Cover Presence + % CWD + % Ground + Veg Density	5	183.10	1.78	0.01
Occurrence ~ Canopy + Cover Presence + % Ground + % Live Woody + Veg Density	5	183.27	1.95	0.01

Top Model Variables (1 x 1 m) - 2D

Parameter	Estimates	SE	Lower 95% CI	Upper 95% CI
Canopy	-0.73	0.35	-1.30	-0.16
Cover Presence	0.52	0.17	0.25	0.80
% Herb	0.36	0.68	-0.76	1.47
% Litter	0.00	0.42	-0.69	0.69
% Bare Ground	-0.40	0.52	-1.26	0.45
% CWD	0.34	0.40	-0.32	0.99
% Live Woody	0.46	0.62	-0.56	1.48
Reed Cover	-0.18	0.18	-0.48	0.11
Veg Density	0.30	0.25	-0.10	0.71

Table 2.8. Resource selection function assessing habitat variables at the exact location scale (1 x 1 m) from a 3-D view as predictors of eastern hog-nosed snake (*Heterodon platirhinos*) occurrence in Huron County. A total of 2048 models were fit for all possible predictor combinations, with only null and top models with ΔAICc ≤ 2 shown. The Akaike's Information Criterion value (AICc) difference from top model in AIC score (ΔAICc), Akaike weights, and number of parameters (K) of the models are included. Estimates, standard errors (SE), ΔAICc, and Akaike weights are presented for model parameters.

Exact Location Model (1 x 1 m) Formula - 3D	K	AIC	ΔAIC	Weight
Occurrence ~ Intercept	0	214.10	31.68	8.09E-12
Occurrence ~ Canopy + Cover Presence + % CWD + % Litter + % Herb + % Live Woody	6	182.41	0.00	0.05
Occurrence ~ Canopy + Cover Presence + % CWD + % Herb + % Live Woody	5	182.43	0.02	0.05
Occurrence ~ Cover Presence + % CWD + % Herb + % Live Woody	4	183.12	0.70	0.03
Occurrence ~ Canopy + Cover Presence + % CWD + % Herb + % Live Woody + Veg Density	6	183.33	0.91	0.03
Occurrence ~ Canopy + Cover Presence + Reed Cover + % CWD + % Litter + % Herb + % Live Woody	7	183.38	0.96	0.03
Occurrence ~ Canopy + Cover Presence + % Ground + % CWD + % Herb + % Woody	6	183.62	1.20	0.03
Occurrence ~ Canopy + Cover Presence + % CWD + % Litter + % Herb + % Live Woody + Veg Density	7	183.63	1.22	0.03
Occurrence ~ Canopy + Cover Presence + Reed Cover + % CWD + % Herb + % Live Woody	6	183.91	1.49	0.02
Occurrence ~ Canopy + Cover Presence + Reed Cover + % CWD + % Litter + % Herb + % Live Woody + Veg Density	8	184.01	1.60	0.02
Occurrence ~ Canopy + Cover Presence + Reed Cover + % CWD + % Herb + % Live Woody + Veg Density	7	184.28	1.86	0.02

Top Model Variables (1 x 1 m) - 3D

Parameter	Estimates	SE	Lower 95% CI	Upper 95% CI
Canopy	-0.79	0.33	-1.34	-0.23
% Herb	0.83	0.33	0.29	1.36
% Litter	0.35	0.27	-0.10	0.80
% Bare Ground	0.04	0.25	-0.38	0.45
% CWD	0.60	0.23	0.22	0.98
% Live Woody	0.60	0.27	0.17	1.05
Cover Presence	0.50	0.17	0.23	0.78
Veg Density	0.08	0.06	-0.02	0.18
Reed Cover	-0.25	0.18	-0.55	0.05

Table 2.9. Resource selection function assessing vegetation variables by height and growth form at the exact location scale (1 x 1 m) as predictors of eastern hog-nosed snake (*Heterodon platirhinos*) occurrence in Huron County, ON. A total of 8192 models were fit for all possible predictor combinations, with only null and top models with ΔAICc ≤ 2 shown. The Akaike's Information Criterion value (AICc) difference from top model in AIC score (ΔAICc), Akaike weights, and number of parameters (K) of the models are included. Estimates, standard errors (SE), ΔAICc, and Akaike weights are presented for model parameters.

Form & Height Model (within 1 x 1 m) Formula	K	AIC	ΔAIC	Weight
Occurrence ~ Intercept	0	227.35	18.77	1.9E-06
Occurrence ~ oneShrub + twoForb + twoGram + twoShrub	4	208.59	0	0.022
Occurrence ~ oneForb + oneShrub + twoForb + twoGram + twoShrub	5	208.93	0.35	0.019
Occurrence ~ twoForb + twoGram + twoShrub	3	209.08	0.49	0.017
Occurrence ~ oneShrub + twoForb + twoGram + twoShrub + threeGram	5	209.21	0.62	0.016
Occurrence ~ oneForb + oneShrub + twoForb + twoGram + twoShrub + threeGram	6	209.40	0.81	0.015
Occurrence ~ threeGram + twoForb + twoGram + twoShrub	4	209.68	1.10	0.013
Occurrence ~ oneGram + oneShrub + twoForb + twoGram + twoShrub	5	209.77	1.18	0.012
Occurrence ~ oneShrub + twoForb + twoGram + twoShrub + twoTree	5	209.95	1.36	0.011
Occurrence ~ twoForb + twoGram + twoShrub + twoTree	4	210.11	1.53	0.010
Occurrence ~ oneGram + twoForb + twoGram + twoShrub	4	210.17	1.59	0.010
Occurrence ~ oneForb + oneGram + oneShrub + twoForb + twoGram + twoShrub	6	210.20	1.62	0.010
Occurrence ~ oneForb + twoForb + twoGram + twoShrub	4	210.27	1.69	0.010
Occurrence ~ oneForb + oneShrub + twoForb + twoGram + twoShrub + twoTree	6	210.33	1.74	0.009
Occurrence ~ oneShrub + twoForb + twoGram + twoShrub + twoTree + threeGram	6	210.41	1.82	0.009
Occurrence ~ oneGram + oneShrub + twoForb + twoGram + twoShrub + threeGram	6	210.47	1.88	0.009
Occurrence ~ twoForb + twoGram + twoShrub + twoTree + threeGram	5	210.53	1.94	0.008

Top Model Variables (Form & Height within 1 x 1 m)

Parameter	Estimates	SE	Lower 95% CI	Upper 95% CI
threeGram	0.17	0.12	-0.02	0.36
twoTree	0.12	0.13	-0.10	0.34
twoShrub	0.45	0.15	0.21	0.69
twoGram	0.60	0.20	0.27	0.93
twoForb	0.79	0.23	0.41	1.17
oneShrub	0.26	0.15	0.01	0.50
oneGram	-0.13	0.17	-0.41	0.15
oneForb	0.24	0.18	-0.05	0.53

Table 2.10. Dunn's post-hoc results of significant differences between thermal habitat types available for use by eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County, ON. Asterisk (*) indicates significant result.

Habitat Type	Beach	Bluff	Coniferous	Deciduous	Old Field	Open Sand	Riparian	Dead PH	Dead RC	Live PH	Live RC
Bluff	*0.46*	-	-	-	-	-	-	-	-	-	-
Coniferous	*<0.05 **	*<0.05 **	-	-	-	-	-	-	-	-	-
Deciduous	*<0.05 **	*<0.05 **	*<0.05 **	-	-	-	-	-	-	-	-
Old Field	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	-	-	-	-	-	-	-
Open Sand	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*0.17*	-	-	-	-	-	-
Riparian	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	-	-	-	-	-
Dead PH	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	-	-	-	-
Dead RC	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	-	-	-
Live PH	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	-	-
Live RC	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	*<0.05 **	-

Table 2.11. Mean ground temperature (°C) of available habitat types for use by eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County, ON. iButton data loggers recorded hourly ground temperatures (°C) during the 2019 and 2020 active seasons.

		Average Temperature (°C) +/- SD			
Habitat	**Locations**	May 19 - June 19	June 20 - July 20	July 21 - Aug 21	Aug 22 - Sept 22
Beach	7	19.47 ± 4.99	23.85 ± 4.56	23.27 ± 3.98	20.05 ± 3.31
Bluff	5	17.80 ± 5.63	22.43 ± 4.20	21.38 ± 2.93	21.70 ± 7.65
Coniferous	7	14.46 ± 3.35	18.91 ± 2.26	19.27 ± 2.05	16.90 ± 2.94
Deciduous	7	15.32 ± 3.04	19.06 ± 1.92	19.55 ± 1.80	17.13 ± 1.67
Old Field	7	19.91 ± 8.18	23.82 ± 7.64	23.96 ± 6.39	19.86 ± 5.69
Open Sand	7	18.77 ± 6.58	23.03 ± 5.96	23.24 ± 4.91	19.28 ± 4.48
Riparian	7	19.56 ± 5.68	23.05 ± 4.96	22.23 ± 3.84	19.45 ± 4.37
Dead PH	10	15.85 ± 4.96	18.79 ± 4.10	20.31 ± 3.73	17.37 ± 2.99
Dead RC	4	17.71 ± 3.98	22.44 ± 4.82	22.25 ± 4.54	18.08 ± 4.39
Live PH	4	15.39 ± 4.18	17.96 ± 2.97	19.49 ± 2.34	17.67 ± 2.59
Live RC	12	15.68 ± 2.47	19.60 ± 3.65	20.00 ± 3.63	17.29 ± 3.87
		17.27 ± 4.82	*21.18 ± 4.28*	*21.36 ± 3.65*	*18.62 ± 4.00*

Table 2.12. Number of eastern hog-nosed snakes (*Heterodon platirhinos*) encountered in Huron County, ON from 2017 to 2020. Data from years marked with an asterisk (*) were collected by the Huron Stewardship Council.

Year	New Captures (#)	Recapture from Previous Years (#)	Within Year Recapture (#)	Total Capture (#)
***2017**	12	0	0	12
***2018**	15	0	24	39
2019	12	3	0	15
2020	2	3	0	5
	41	**6**	**24**	**71**

Table 2.13. Age class, sex, PIT-tag status, and mortality of eastern hog-nosed snakes (*Heterodon platirhinos*) upon a first encounter from 2018 to 2020 (n = 29) in Huron County, ON.

Age Class	Status (%)		Sex (%)			Tagged (%)
	Live	Deceased	Male	Female	Unknown	
Adult (n = 15)	100	0	33	67	0	64
Sub-adult (n = 10)	100	0	40	40	20	90
Juvenile (n = 1)	100	0	0	0	100	100
Neonate (n = 3)	33	67	0	0	3	0

Table 2.14. Deceased eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County observed from 2018 to 2020 (n = 9), organized by age class, year, and cause of death (natural = N or human-caused = H). *All other age classes in which deceased individuals were not observed are not listed.

Cause of Death	2018 Neonate (n = 2)	2018 Adult (n = 5)	2019 Adult (n = 0)	2020 Adult (n = 2)
Vegetation Management (H)	0%	20%	0%	0%
Surgery Complication (H)	0%	20%	0%	0%
Road Mortality (H)	100%	0%	0%	0%
Agriculture Operations (H)	0%	0%	0%	50%
Predation (N)	0%	60%	0%	50%

Appendix 2B

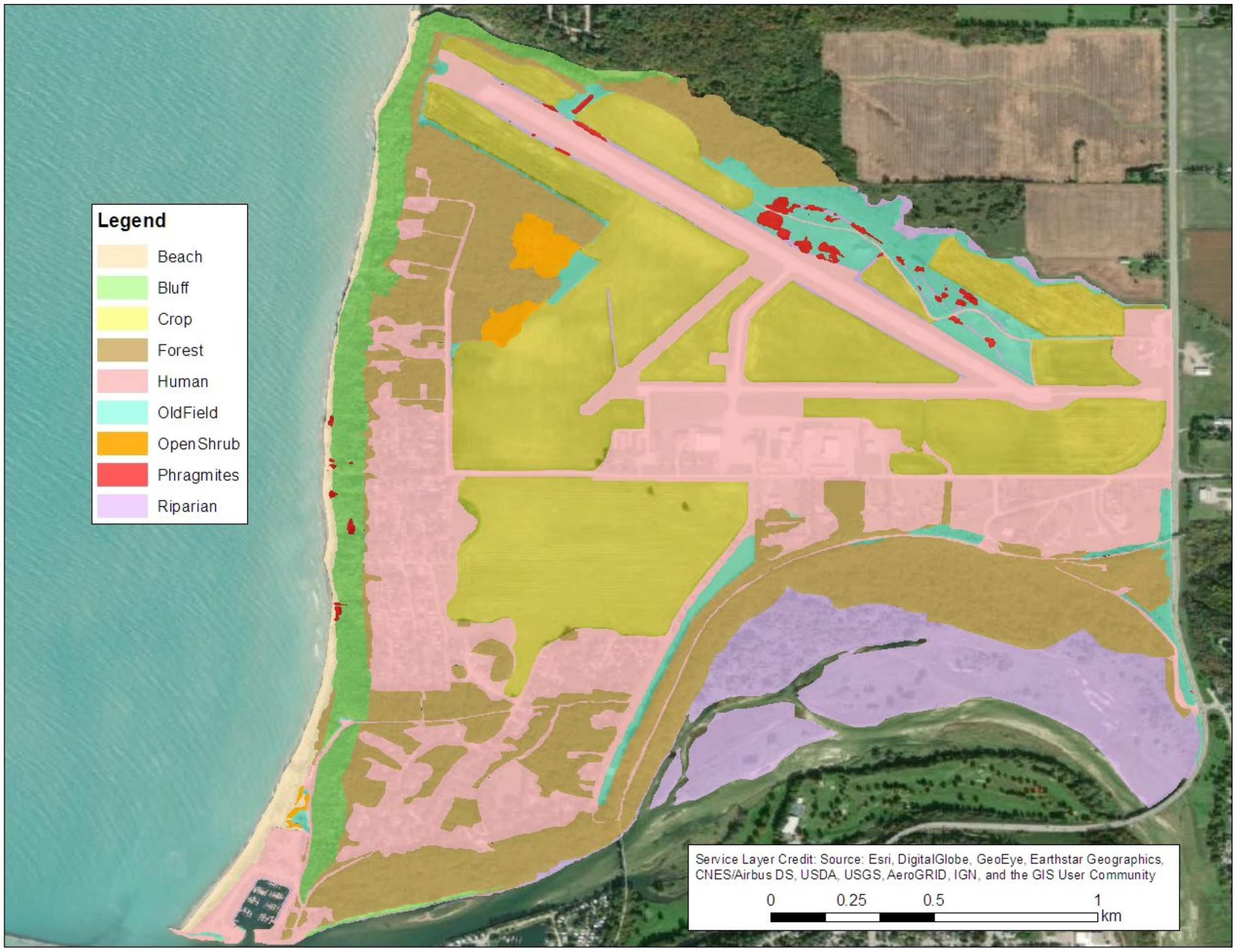

Figure 2.1 Habitat types available for use by eastern hog-nosed snakes (*Heterodon platirhinos*) within Huron County, ON. Habitat polygons were digitized and delineated in ArcMap (v. 10.5.1; ESRI 2021) by referencing aerial imagery (0.2 m^2 resolution, Huron County 2015; CNES 2020).

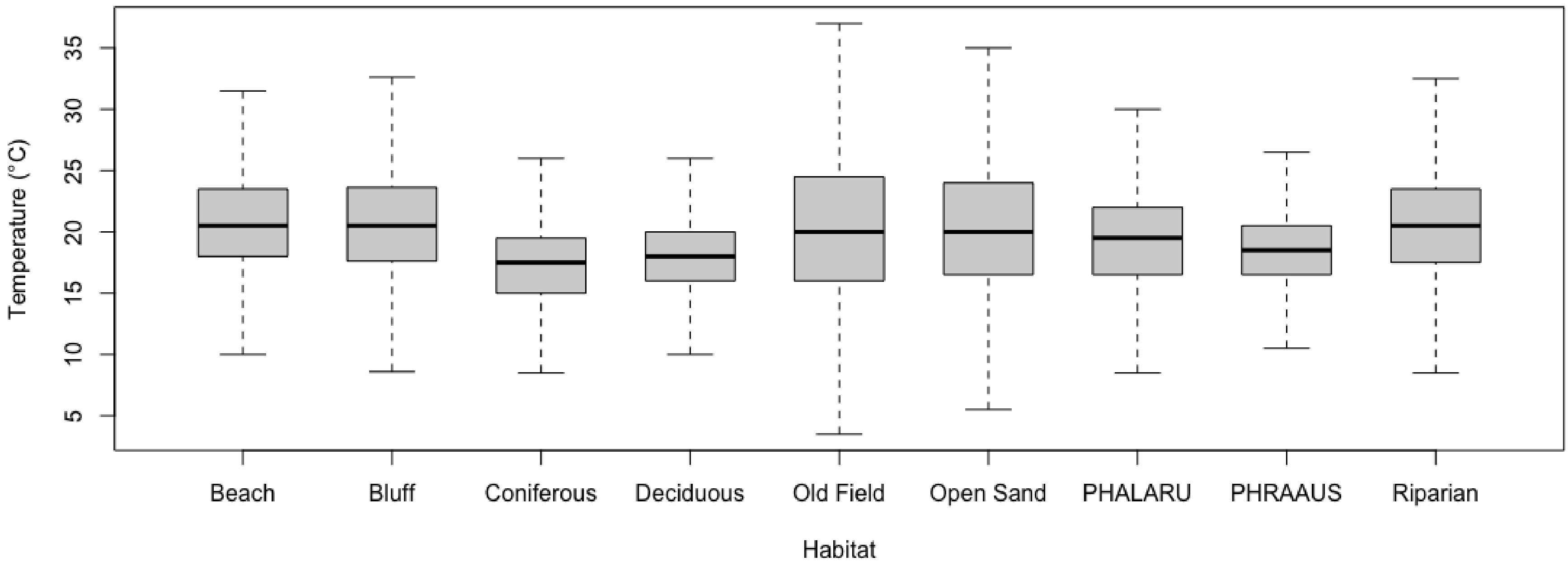

Figure 2.2. Mean ground temperature (°C) of habitat types available to eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County, ON recorded during the active season of 2019 and 2020. Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

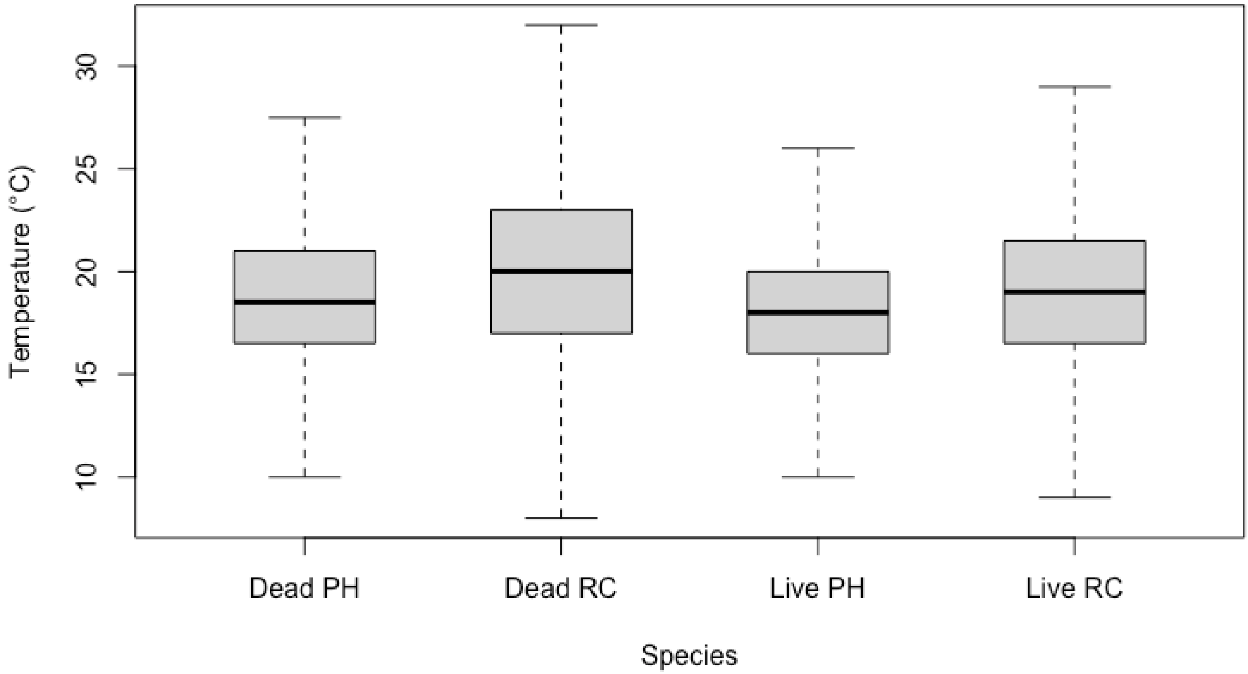

Figure 2.3. Mean ground temperature (°C) of live and standing dead reed canary (*Phalaris arundinacea*; RC; n = 4) and *Phragmites* (*Phragmites a. australis*; PH; n = 10) invasive grass stands in Huron County, ON. Temperatures recorded using iButton temperature loggers during the active seasons of 2019 and 2020. Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

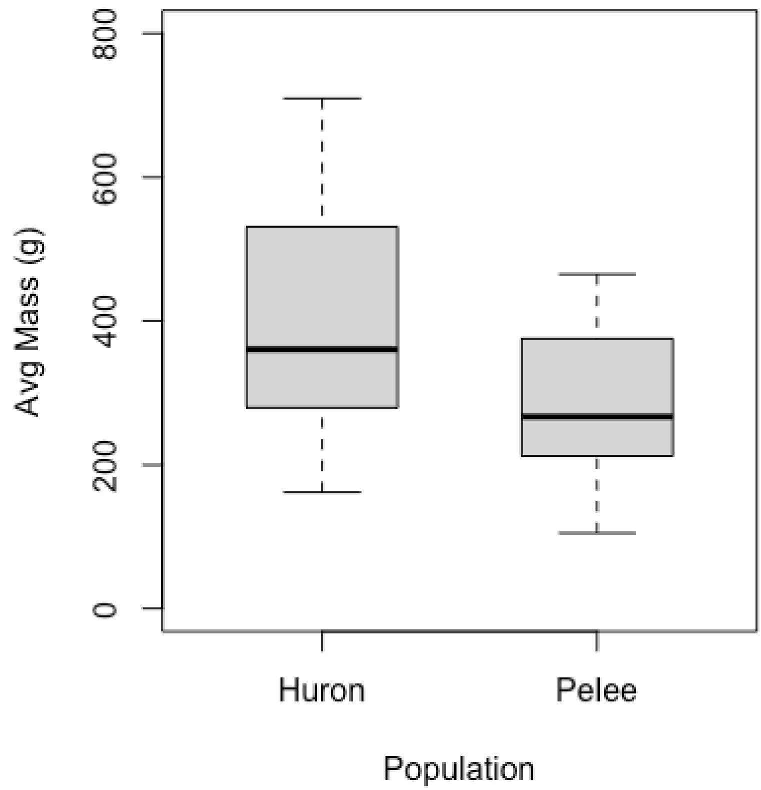

Figure 2.4. Mean mass (g) of sub-adult and adult eastern hog-nosed snakes (*Heterodon platirhinos*) by population (Huron n = 17, Pelee n = 20). Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

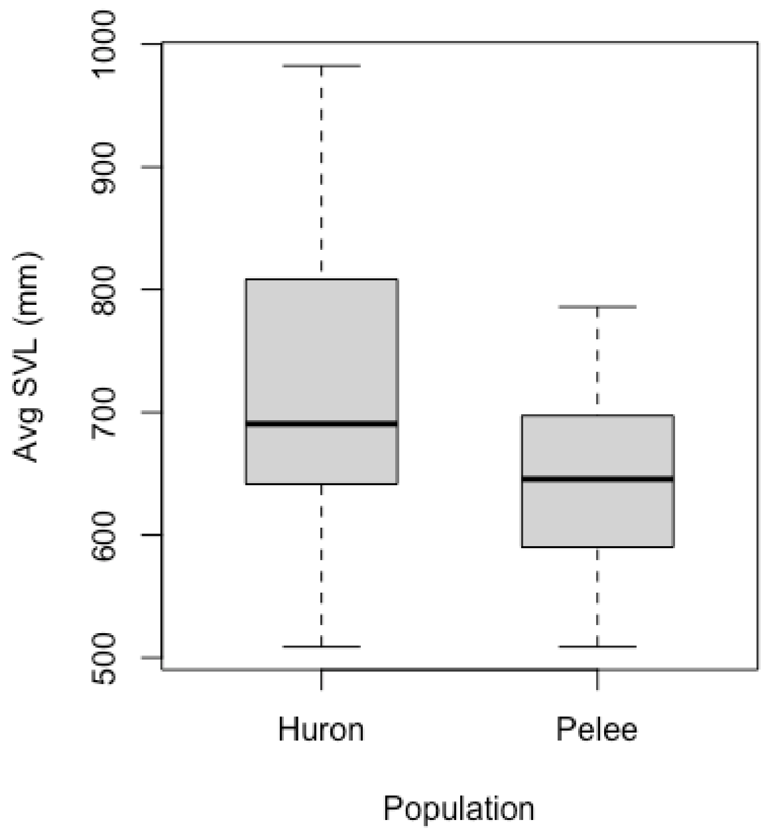

Figure 2.5. Mean snout-vent length (SVL; mm) of sub-adult and adult eastern hog-nosed snakes (*Heterodon platirhinos*) by population (Huron n = 17, Pelee n = 20). Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

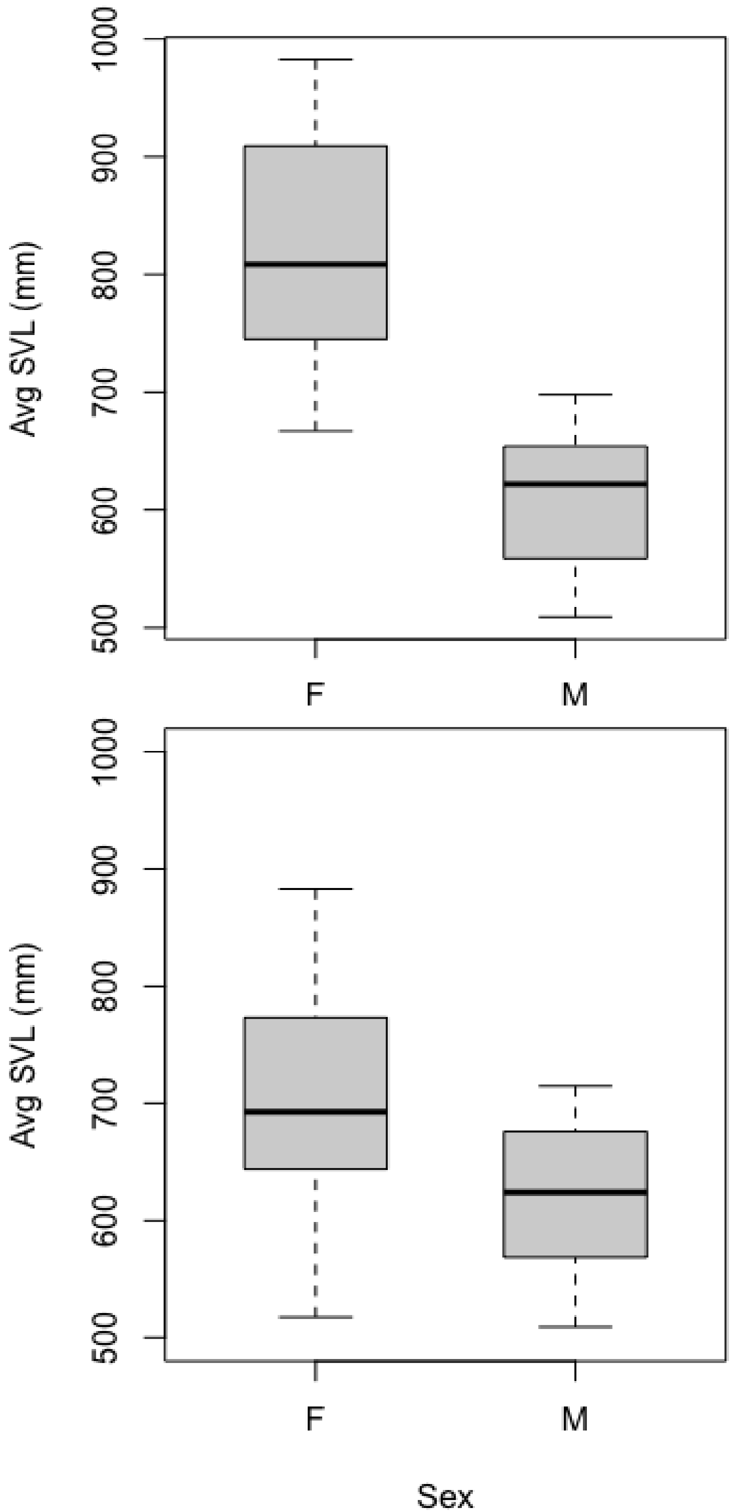

Figure 2.6. Mean snout-vent length (SVL; mm) by sex (F = Female, M = Male) of sub-adult and adult eastern hog-nosed snakes (*Heterodon platirhinos*) for Huron County (top panel; Female n = 9, Male n = 8) and Pelee (bottom panel; Female n = 8, Male n = 12). Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

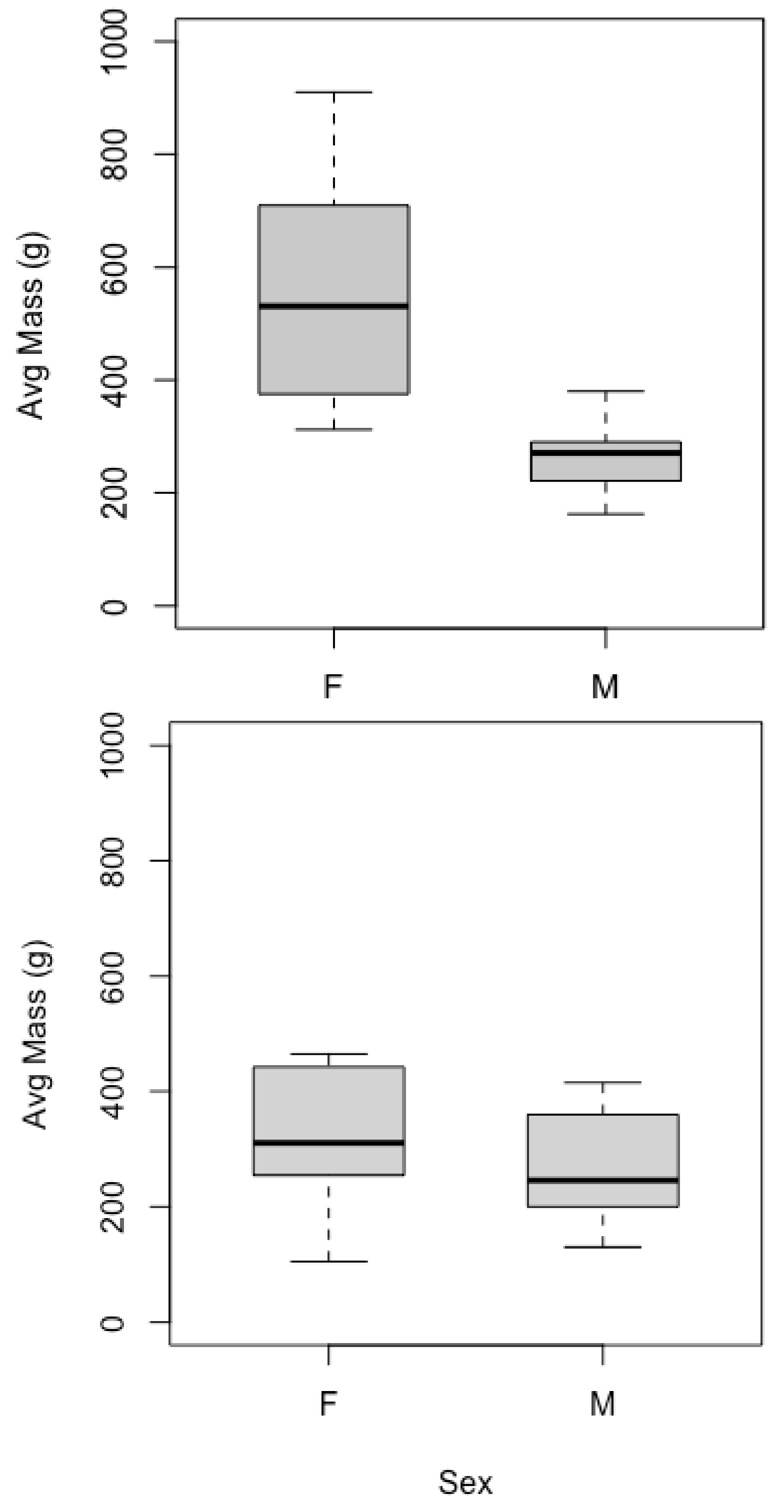

Figure 2.7. Mean mass (g) by sex (F = Female, M = Male) of sub-adult and adult eastern hog-nosed snakes (*Heterodon platirhinos*) for Huron County (top panel; Female n = 9, Male n = 8) and Pelee (bottom panel; Female n = 8, Male n = 12). Boxes represent 25^{th} to 75^{th} percentiles; solid lines within each box represent medians; whiskers are ranges.

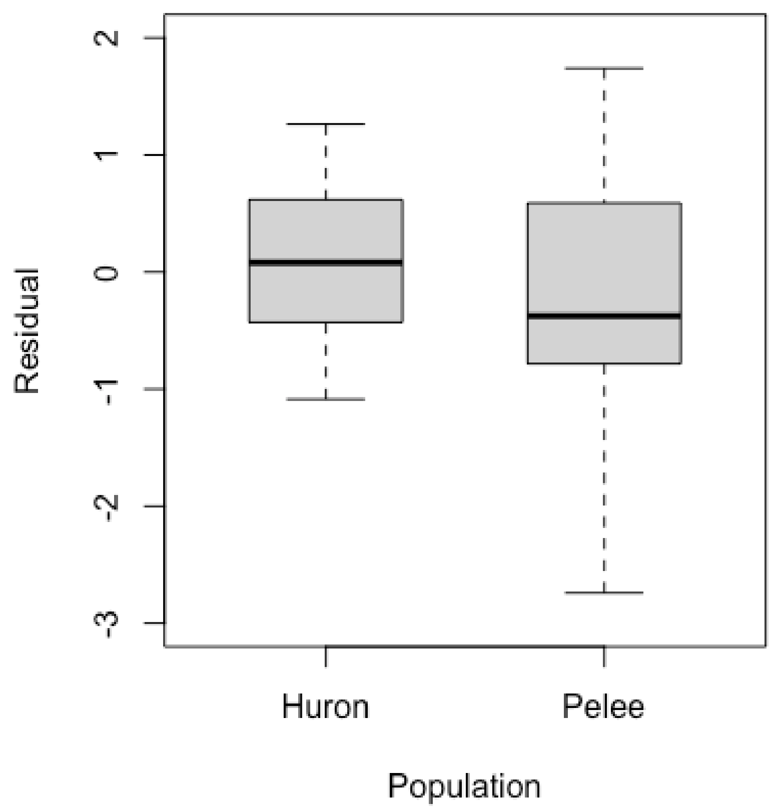

Figure 2.8. Residuals of log(10) transformed snout-vent length (SVL) by log(10) transformed mass regression representing body condition for each population of eastern hog-nosed snake (*Heterodon platirhinos*) (Huron n = 17, Pelee n = 20). Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

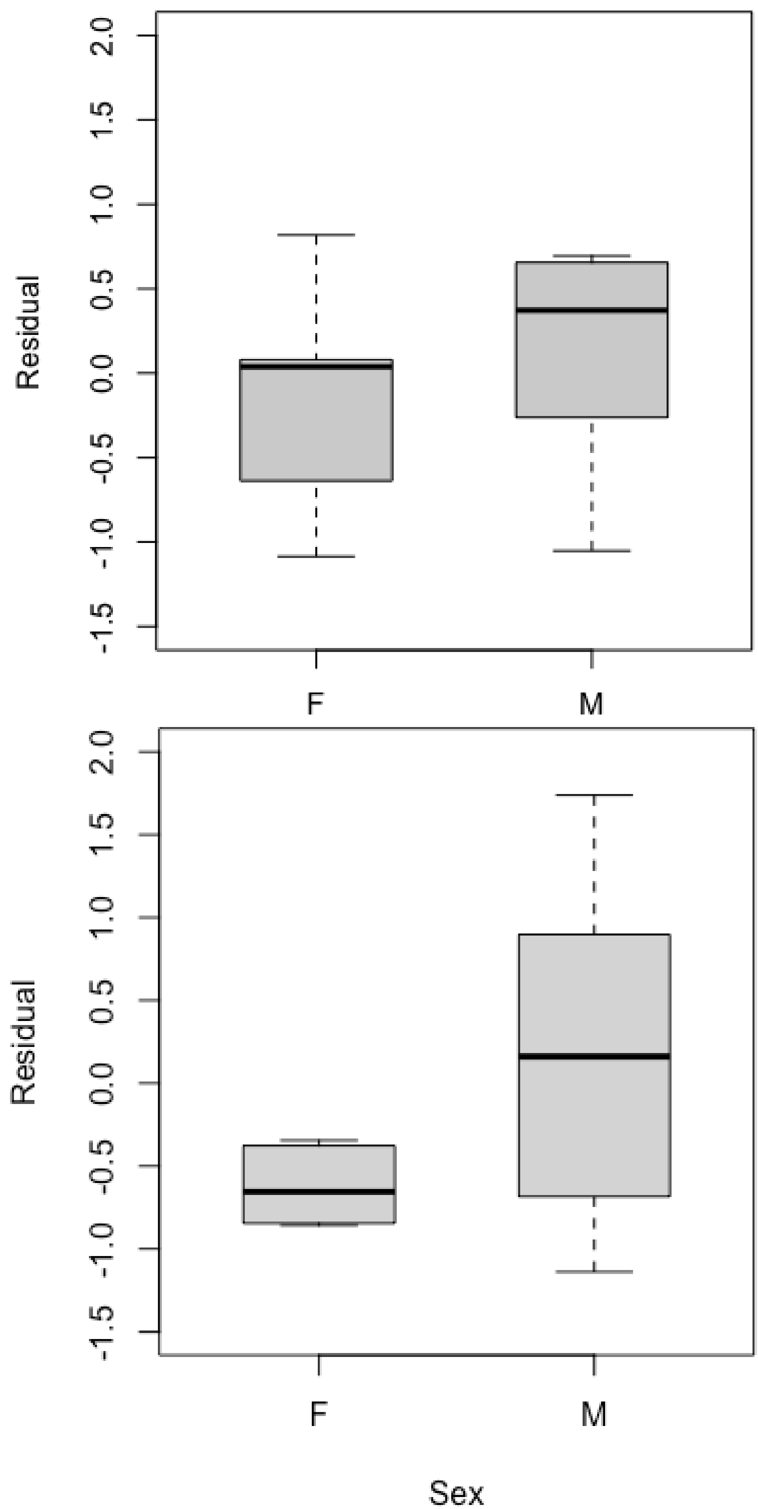

Figure 2.9. Residuals of log(10) transformed snout-vent length (SVL) by log(10) transformed mass regression, representing body condition by sex (F = Female, M = Male) for eastern hog-nosed snakes (*Heterodon platirhinos*) in Huron County (top panel; Female n = 9, Male n = 8) and Pelee (bottom panel; Female n = 8, Male n = 12). Boxes represent 25th to 75th percentiles; solid lines within each box represent medians; whiskers are ranges.

General Conclusions and Management Implications

My research contributes to the recovery and protection of a recently reported population of eastern hog-nosed snakes, a provincially and federally Threatened species (Kraus 2011; COSEWIC 2021). Results of this project fulfill government-mandated recovery actions outlined for the species in the provincial Government Response Statement (OMNRF 2016). Objectives of my project align with multiple branches of provincial government-supported actions that are considered necessary to the success of protecting and recovering eastern hog-nosed snakes in Ontario. These actions include: 1) inventory and monitoring to increase knowledge about the presence, distribution, and abundance over time of eastern hog-nosed snakes in Ontario, 2) management by identifying critical habitats including nesting sites and hibernacula, 3) research on the species in Ontario, 4) increasing habitat connectivity, and 5) assessment of specific threats to habitat (OMNRF 2016). The results from my research have created a foundation to continue monitoring the integrity of the population of eastern hog-nosed snakes in Huron County and their critical habitat over time. Gaps in baseline knowledge for the recently-reported population in Huron County have been filled, with a better understanding of the spatial ecology and habitat preferences, thus contributing to the greater breadth of knowledge required for successful recovery of eastern hog-nosed snakes across Ontario.

My research was the first to examine spatial ecology and general habitat selection by eastern hog-nosed snake in Huron County, Ontario, a highly modified landscape that appears to influence space use and habitat requirements of the species. While natural habitats exist within the study area, anthropogenic activity is widespread, and hog-nosed snakes appear to be adjusting their space use in response to human activity. Beach, forest, and old field habitats were preferred by hog-nosed snakes, while anthropogenic, bluff, cropland, and riparian habitats were often avoided. With snake movement largely demonstrating avoidance of heavily modified areas, mean distance moved per day and home range size of Huron County individuals were greater than most other North American populations (Lagory et al. 2009; Robson 2011; Akresh et al. 2017; Buchanan et al. 2017; Vanek and Wasko 2017). As such, what remains of natural habitats in the Huron County area appear critical for hog-nosed snakes to fulfill their daily and seasonal requirements, and to support the persistence of the species within the modified landscape. Natural habitats such as the beach and lake bluff-side appear important for population persistence, as both are overwintering habitat, and the beach provides the only known nesting area for the population. Maintaining the integrity of existing natural areas will be imperative to ensuring that this population of eastern hog-nosed snakes continues to persist in Huron County.

In Huron County, structural complexity and thermal suitability are important elements to habitat selection by eastern hog-nosed snakes. Hog-nosed snakes preferred structurally complex habitats as they afforded snakes cover, thermal suitability, and refuge. For snakes, thermal quality is key to habitat suitability (Pringle et al. 2003) and a driver in habitat selection (Huey et al. 1989; Reinert 1993; Blouin-Demers and Weatherhead 2001a, b, c). Thus, structural complexity can be a crucial element to thermal habitat quality, as ground temperatures can vary significantly with vegetation structure (Newbold and MacMahon 2014). Non-native vegetation can threaten both structural complexity and thermal resources available for reptiles (Bolton and Brooks 2010; Carter et al. 2015; Cook et al. 2018; Markle et al. 2018). As such, I expected that invasive grass species, reed canary (*Phalaris arundinacea*) and *Phragmites* (*Phragmites a. australis*), would impact quality and availability of thermal habitat for hog-nosed snakes, but found that only *Phragmites* was poor thermal habitat. While reed canary and *Phragmites* are known to have negative ecological impacts (Weinstein and Balletro 1999; Bolton and Brooks

2010; OMNR 2011; Markle et al. 2018), the warmer and more variable thermal profile of reed canary makes it thermally suitable and contributes to Huron County's thermal habitat mosaic, even if reed canary may not be structurally or thermally optimal compared to some natural habitats. While hog-nosed snakes are known to use a variety of habitats (Seburn 2009), availabilities of structurally complex and thermally suitable habitats are vital to space use by eastern hog-nosed snakes in Huron County.

Although a population of eastern hog-nosed snakes manages to persist within the modified landscape of Huron County, anthropogenic activity pushes the limits of snake survival and exacerbates threats faced by this population located at the species' range periphery. While human activity does not appear to increase mortality rates of hog-nosed snakes in Huron County compared to snakes in other locations (Plummer and Mills 2000; Robson 2011; Rouse et al. 2011; Buchanan 2012), nor does it appear to impact body condition, individuals in Huron County face a unique and diverse suite of threats including residential and commercial development, aviation infrastructure, and agriculture. Even recreational activities within Huron County, that would otherwise be considered low-impact, threatened hog-nosed snake survival. For example, while the trail system running though the study site does not fully impede snake movement, it poses a potentially detrimental risk for snakes when they intersect the trails. While no fatal incidents between snakes and cyclists occurred during the study period, hog-nosed snakes crossing the trail system would be difficult to notice and avoid while cycling. Burning washed up driftwood along the lakeshore also poses a threat to Huron County's eastern hog-nosed snakes. For example, in 2019 a radio-tagged female sought shelter around a single large driftwood trunk for a few weeks while she was gravid and preparing for ecdysis. During this period, beachgoers had used a different washed-up trunk, less than 3 meters from the pregnant female's log, for a bonfire. By happen-stance the gravid female's 'chosen' log had not been burned, but if it had, she would have been severely at risk, since female snakes rarely move or feed when gravid (Graves and Duvall 1993; Plummer 1997; Parent and Weatherhead 2000), to fulfill energetic demands required by developing offspring (Shine 2003) and pre-oviposition ecdysis (Reinecke et al. 1980; Gaban and Farley 2002; Clayton 2012). Thus, although eastern hog-nosed snakes persist and do not appear imminently threatened by anthropogenic activity, Huron County's modified landscape exacerbates pre-existing pressures that threaten hog-nosed snake survival.

The integrity of eastern hog-nosed snake critical habitat is also under anthropogenic pressure. Suitable hibernacula and nesting habitat are recognized as critical components to ensuring eastern hog-nosed snake persistence (Seburn 2009; Kraus 2011) and are noted as limiting factors for the species in Canada (COSEWIC 2007). However, for hog-nosed snake populations in southern Ontario where habitat loss is a primary threat to biodiversity (Ontario Biodiversity Council 2011) and natural areas are highly fragmented (Seburn 2009), suitable critical habitat can be limited. While natural areas exist in Huron County, they are highly fragmented by anthropogenic activity, thus limiting the ability and success of hog-nosed snakes to carry out basic life requirements. The Huron County study site consists of a single stretch of dune habitat, approximately 80 m long, that supports foraging, all nesting activity (the only area to have nesting activity in all three years of data collection) and a known hibernaculum. The area also supports the critical period prior to nesting, as a pre-oviposition staging area, where gravid females thermoregulate within 100 m of their oviposition site (G. Cunnington pers. comm.). While occurrence of critical foraging, nesting, pre-oviposition, and overwintering activity within the dune habitat attests to the quality and importance of this area, anthropogenic activity predominantly surrounds it. Of a list of activities likely to destroy critical habitat outlined in the species' federal recovery strategy (Seburn 2009), four out of the five examples (road construction, development, vegetation removal, off-road vehicle use in nesting areas) were observed within proximity of dune habitat. For example, in 2018 and 2019, beachgoers parked vehicles directly upon or adjacent to the dune area. Snake awareness signage and temporary barriers were placed to prevent access in 2019; however, signage was vandalized the following year. In 2020 other instances included unpermitted native vegetation removal and widening of the existing marina road to accommodate future development. While this is not the first eastern hog-nosed snake population to experience destructive activities within critical habitat (Robson 2011; G. Cunnington pers. comm. 2019; S. Gillingwater pers. comm. 2020; COSEWIC 2021), anthropogenic threats that destroy the only known nesting area for the population could lead to extirpation due to direct mortality of gravid females and lack of recruitment.

Habitat fragmentation is forcing individuals to congregate in small areas. In one population of eastern hog-nosed snakes in Wasaga Beach, ON gravid females aggregated at oviposition sites and nested communally (Cunnington and Cebek 2005). Communal nesting was attributed to limited availability of oviposition habitat within the heavily modified site (Cunnington and Cebek 2005), where only 1.3% of the total area in Wasaga Beach was suitable for nesting (G. Cunnington pers. comm.). Similar to females of Wasaga Beach that communally nested, females at the Huron County study site also clustered their oviposition activity within a single area of high-quality habitat. While clustering for a chance at successful oviposition amongst the heavily modified landscape, numerous individuals simultaneously inhabiting a single area and exclusively relying on it to complete their reproductive cycle could potentially compromise population persistence. For example, as a result of a major slumping event at a single communal snake den in Grasslands National Park, Canada (Gardiner and Sonmor 2011), there was a 50% decrease in the local eastern yellow-bellied racer population (*Coluber constrictor flaviventris*) (Martino and Gardiner unpublished data). Mass mortality events can impact population structure and viability and have the potential to cause extirpation and genetic isolation, particularly in peripheral populations (Parent and Weatherhead 2000; Young and Clarke 2000; COSEWIC 2004). Thus, it will be critical to protect and maintain the integrity of dune habitat for eastern hog-nosed snakes in Huron County. In alignment with government-mandated recovery actions outlined by the provincial government (OMNRF 2016), I recommend that along the marina road, an important corridor to access dune habitat, wildlife exclusion fencing and eco-passages be installed. While there has been great success in using exclusion fences and eco-passages to redirect reptile movement and help reduce road mortality (Colley 2015), mechanics and materials of this mitigation strategy can also be problematic. For example, if fencing integrity is not maintained, reptiles can get stuck in the fencing or get trapped on the road side of the fence when individuals cannot find a complementary 'hole' in the fence to exit the road surface (Baxter-Gilbert et al. 2015). Thus, there is a long-term commitment with implementing this mitigation strategy in that fencing must be maintained. As it is a private road, stakeholders may not be willing to incur the costs and maintenance long-term, so discussions between appropriate stakeholders and the Huron Stewardship Council may be required to create a long-term plan and agreement.

Limitations and Future Research

While human activity and natural processes influenced the survival and sample size of hog-nosed snakes observed during my study, the relatively small sample size was exacerbated due to the COVID-19 pandemic in 2020. Issues due to the on-set of the pandemic included, but were not limited to, reduced site access, decreased community engagement, and delayed permit release. For example, surveys during optimal survey periods, post-overwintering emergence and nesting season, were delayed due to limited site access and the delayed issuance of provincial handling permits. The various obstacles encountered during the 2020 active season reduced encounters with snakes, thus impacting overall sample size. The season prior to the pandemic, number of surveyors were limited, and it had been planned for the 2020 season to try and engage members of the community to assist with visual encounter surveys during optimal survey periods. While I was not able to employ this strategy during the 2020 season, I would still recommend that for a larger sample size and to effectively continue to monitor the population in the future, increasing the number of surveyors is recommended. The best chance at detecting this already cryptic species appears to require multiple sets of eyes from various surveyors.

Knowledge gaps remain as to whether eastern hog-nosed snake movement and habitat selection are influenced by crop type. The response by reptiles with respect to crop type appears to vary. In one study, percentage of hay was a predictor variable in explaining grassland snake occurrence along roads, while cropland was not (Fortney et al. 2012). In others, crop type has been documented to influence symmetry, distance, and orientation of reptile movement (Kay et al. 2016; Rotem and Ziv 2016) and even juvenile dispersal (Rotem and Ziv 2016). Thus, for a mobile species like the eastern hog-nosed snake (COSEWIC 2007), crop type may have a significant impact on movement. During my study, type of crop planted differed by year, with crop type composed of either wheat or soy. During the years that soy was planted (2018 and 2020), no radio-tracked snakes used the crop fields, while in 2019 snakes were located within wheat fields. Although some radio-tracked snakes were located within cropland, I was unable to directly quantify whether crop type was influential to eastern hog-nosed snake habitat selection and quality. Stem-lines and subsequent lines of sight influence animal movement within cropland (Prevedello and Vieira 2010; Sozio et al. 2013; Kay et al. 2016) and the noticeable differences in growth form and structure (pers. observ.) between soy and wheat (broad-leaved forb and grass, respectively) would likely influence movement of hog-nosed snakes, in addition to the likely variation in structural and thermal quality of different crop types.

Because radio-tracked eastern hog-nosed snakes moved across the recreational trail system that runs through the Huron County study side, it appears that this form of anthropogenic activity does not impede snake movement. However, it remains unknown how the type of trail activity and frequency of human use impacts hog-nosed snakes. In one study, all 13 species of wildlife detected along mountain trails demonstrated avoidance of all recreational activities, and temporal avoidance was greatest towards mountain bike activity (Naidoo and Burton 2019). In another study, human activity along pathways influenced basking behaviour of northern water snakes (*Nerodia sipedon*), where number of pedestrians and type of activity (e.g., walking, jogging) influenced response time of snake retreat behaviour (Burger 2001). Thus, while habitat use by eastern hog-nosed snakes overlaps with the trail system, how and when snakes use trails may be dependent upon type and frequency of human activities on the trail and would be of interest to examine for future research.

Literature Cited

Akresh, M.E., King, D.I., Timm, B.C., and Brooks, R.T. 2017. Fuels management and habitat restoration activities benefit eastern hognose snakes (*Heterodon platirhinos*) in a disturbance-dependent ecosystem. Journal of Herpetology **51**(4): 468-476.

Baxter-Gilbert, J.H., Riley, J.L., Lesbarrères, D., Litzgus, J.D. 2015. Mitigating reptile road mortality: fence failures compromise ecopassage effectiveness. PloS One **10**(3): 1-15.

Blouin-Demers, G. and Weatherhead, P.J. 2001a. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology **82**: 3025-3043.

Blouin-Demers, G., and Weatherhead, P.J. 2001b. An experimental test of the link between foraging, habitat selection and thermoregulation in black rat snakes *Elaphe obsoleta obsoleta*. Journal of Animal Ecology **70**: 1006-1013.

Blouin-Demers, G. and Weatherhead, P.J. 2001c. Habitat use by black rat snakes (*Elaphe obsolete obsoleta*) in fragmented forest. Ecology **82**: 2882-2896.

Bolton, R.M., and Brooks, R.J. 2010. Impact of the seasonal invasion of *Phragmites australis* (Common Reed) on turtle reproductive success. Chelonian Conservation and Biology **9**: 238-243.

Buchanan, S.W. 2012. Ecology of the eastern hognose snake (*Heterodon platirhinos*) at Cape Cod National Seashore, Barnstable County, Massachusetts. M.Sc. Thesis, Biology, Montclair State University, Montclair, New Jersey.

Buchanan, S.W., Timm, B.C., Cook, R.P., Couse, R., and Hazard, L.C. 2017. Spatial ecology and habitat selection of eastern hognose snakes. Journal of Wildlife Management **81**(3): 509-520.

Burger, J. 2001. The behavioral response of basking Northern water (*Nerodia sipedon*) and Eastern garter (*Thamnophis sirtalis*) snakes to pedestrians in a New Jersey park. Urban Ecosystems **5**(2): 119-129.

Carter, E.T., Eads, B.C., Ravesi, M.J., and Kingsbury, B.A. 2015. Exotic invasive plants alter thermal regimes: implications for management using a case study of a native ectotherm. Functional Ecology **29**: 683-693.

Clayton, J. 2012. Care and Breeding the Western Hog-nosed Snake. Available from: https://www.reptilesmagazine.com/care-and-breeding-the-western-hog-nosed-snake/ [Accessed 02 January 2021].

Colley, M. 2015. Eastern Massasauga Rattlesnake: Evaluating the Effectiveness of Mitigation Structures at the Population Level. M.Sc. thesis, Biology, Laurentian University, Sudbury, ON.

Cook, C.E., McCluskey, A.M., Chambers, R.M. 2018. Impacts of invasive *Phragmites australis* on diamondback terrapin nesting in Chesapeake Bay. Estuaries and Coasts **41**: 966-973.

COSEWIC. 2004. COSEWIC Assessment and Status Report on the Eastern and Western Yellow-bellied Racers, *Coluber constrictor flaviventris* and *Coluber constrictor mormon* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vii + 35pp.

COSEWIC. 2007. COSEWIC Assessment and Update Status Report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. viii + 36 pp.

COSEWIC. 2021. COSEWIC Assessment and Update Status Report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xi + 45 pp.

Cunnington, G.M. and Cebek, J.E. 2005. Mating and nesting behavior of the eastern hognose snake (*Heterodon platirhinos*) in the northern portion of its range. American Midland Naturalist **154**(2): 474-478.

Fortney, A.N., Poulin, R.G., Martino, J.A., Parker, D.L., and Somers, C.M. 2012. Proximity to hibernacula and road type influence potential road mortality of snakes in southwestern Saskatchewan. Canadian Field-Naturalist **126**(3): 194-203.

Gaban, R.D. and Farley, R.D. 2002. Ecdysis in scorpions: supine behavior and exuvial ultrastructure. Invertebrate Biology **121**(2): 136-147.

Gardiner, L.E., and Sonmor, K.W. 2011. Major slump event at Grasslands National Park Snake Pit in southwestern Saskatchewan. Blue Jay **69**: 120-124.

Graves, B.M. and Duvall, D. 1993. Reproduction, rookery use, and thermoregulation in free-ranging, pregnant *Crotalus v. viridis*. Journal of Herpetology **27**: 33-41.

Huey, R.B., Peterson, C.R., Arnold, S.J. and Porter, W. 1989. Hot rocks and not-so-hot rocks: retreat site selection by garter snake and its thermal consequences. Ecology **70**: 931-934.

Kay, G.M., Driscoll, D.A., Lindenmayer, D.B., Pulsford, S.A., and Mortelliti, A. 2016. Pasture height and crop direction influence reptile movement in an agricultural matrix. Agriculture, Ecosystems and Environment **235**: 164-171.

Kraus, T. 2011. Recovery Strategy for the Eastern Hog-nosed Snake (*Heterodon platirhinos*) in Ontario. Ontario Recovery Strategy Series. Prepared for the Ontario Ministry of Natural Resources, Peterborough, Ontario. i + 6 pp. + Appendix vi + 24 pp. Adoption of the Recovery Strategy for the Eastern Hog-nosed Snake (*Heterodon platirhinos*) in Canada (Seburn, 2009).

Lagory, K.E., Walston, L.J., Goulet, C., Van Lonkhuyzen, R.A., Najjar, S., and Andrews, C. 2009. An examination of scale-dependent resource use by eastern hognose snakes in Southcentral New Hampshire. Journal of Wildlife Management **78**(3): 1387-1393.

Markle, C.E., Chow-Fraser, G., and Chow-Fraser, P. 2018. Long-term habitat changes in a protected area: Implications for herpetofauna habitat management and restoration. PLoS ONE **13**(2): 1-15.

Maslow, A.H. 1943. A theory of human motivation. Psychological Review **50**: 370-396.

Naidoo, R., and Burton, A.C. 2019. Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. Conservation Science and Practice **2**(10): 1-10.

Newbold, T.A.S., and MacMahon, J.A. 2014. Determinants of habitat selection by desert horned lizards (*Phyrnosoma platyrhinos*): The importance of abiotic factors associated with vegetation structure. Journal of Herpetology **48**(3): 306-316.

OMNR. 2011. Invasive *Phragmites*—Best Management Practices. Ontario Ministry of Natural Resources. Peterborough, ON. Version 2011. 15pp.

OMNRF. 2016. Eastern Hog-nosed Snake Government Response Statement. Ontario Ministry of Natural Resources and Forestry, Species Conservation Policy Branch. Peterborough, ON. 6 pp.

Ontario Biodiversity Council. 2011. Ontario's Biodiversity Strategy, 2011: Renewing Our Commitment to Protecting What Sustains Us. Ontario Biodiversity Council, Peterborough, ON. vi + 69 pp.

Parent, C., and Weatherhead, P. J. 2000. Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. Oecologia **125**(2): 170-178.

Plummer, M.V. 1997. Speed and endurance of gravid and nongravid green snakes *Opheodrys aestivus*. Copeia **1994**: 191-194.

Plummer, M.V., and Mills, N.E. 2000. Spatial ecology and survivorship of resident and translocated hognose snakes (*Heterodon platirhinos*). Journal of Herpetology **34**(4): 565-575.

Prevedello, J.A., and Vieira, M.V. 2010. Plantation rows as dispersal routes: a test with didelphid marsupials in the Atlantic Forest, Brazil. Biological Conservation **143**: 131-135.

Pringle, R.M., Webb, J.K., and Shine, R. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. Ecology **84**: 2668-2679.

Reinecke, J.P., Buckner, J.S., and Grugel, S.R. 1980. Life cycle of laboratory-reared tobacco hornworms, *Manduca sexta*, a study of development and behavior, using time-lapse cinematography. Biological Bulletin **158**(1): 129-140.

Reinert, H.K. 1993. Habitat selection in snakes. *In* Snakes: Ecology and Behaviour. *Edited by* R.A. Seigel & J.T. Collins, The Blackburn Press, Caldwell. pp. 201-240.

Robson, L.E. 2011. The spatial ecology of eastern hognose snakes *(Heterodon platirhinos*): habitat selection, home range size, and the effect of roads on movement patterns. M.Sc. thesis, Biology, University of Ottawa, Ottawa, Ontario.

Rotem, G. and Ziv, Y. 2016. Crop diversity and rotation may increase dispersal opportunities of reptiles in a heterogeneous agroecosystem. Agriculture, Ecosystems & Environment **235**(1): 32-37.

Rouse, J.D., Wilson, R.J., Black, R., and Brooks, R.J. 2011. Movement and spatial dispersion of *Sisturus catenatus* and *Heterodon platirhinos*: Implications for interactions with roads. Copeia **2011**(3): 443-456.

Seburn, D. 2009. Recovery Strategy for the Eastern Hog-nosed Snake (*Heterodon platirhinos*) in Canada. *Species at Risk Act* Recovery Strategy Series. Parks Canada Agency, Ottawa, ON, 24 pp.

Shine, R. 2003. Reproductive strategies in snakes. Proceedings of the Royal Society B **270**(1519): 995-1004.

Sozio, G., Mortelliti, A., and Boitani, L. 2013. Mice on the move: wheat rows as a means to increase permeability in agricultural landscapes. Biological Conservation **165**: 198-202.

Vanek, J.P., and Wasko, D.K. 2017. Spatial ecology of the eastern hog-nosed snake (*Heterodon platirhinos*) at the northeastern limit of its range. Herpetological Conservation and Biology **12**: 109-118.

Weinstein, M.P., and Balletro, J.H. 1999. Does the common reed, *Phragmites australis*, affect essential fish habitat? Estuaries **22**: 793-802.

Young A. and Clarke, G. (eds). 2000. Genetics, Demography and the Viability of Fragmented Populations. Cambridge University Press: Cambridge, UK.