Habitat use by northwestern gartersnakes (*Thamnophis ordinoides*) in Saanich, British Columbia

by

Graham Dixon-MacCallum
BSc., Acadia University, 2008

A Masters Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of

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in the Department of Biology

Supervisory Committee

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Abstract

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Understanding habitat requirements of species is fundamental for their conservation. Comparing habitat variables measured at locations where animals are found to random locations is one method of understanding how a species uses its habitat non-randomly. Northwestern gartersnakes (*Thamnophis ordinoides*) are common in parks in Victoria, but their specific habitat requirements are poorly understood. Victoria's parks vary in habitat composition from mature Douglas-fir forest to Garry Oak meadow, with open grassy areas, to parking lots and patches of dense invasive shrubs. Based on previous studies and thermoregulatory needs of snakes, I predicted that substrate temperature and distance to edge would be of greatest importance in determining where snakes would be found. From May to September, 2012 I captured 124 northwestern gartersnakes by hand on random transects and habitat edge surveys. At capture locations and randomly chosen points nearby I measured the composition and structure of vegetation, as well as abiotic factors such as substrate temperature, aspect and slope. Also, I used air photos and GIS to determine proportional use of broad habitat types at home range scale. I found differential use of habitat between the sexes in relation to the proportion of herbaceous vegetation and organic litter. Northwestern gartersnakes generally use locations that are warmer than random locations, though individuals that have fed recently have a greater thermophilic response than snakes that have not. Overall, at small scale, distance to edge was the most important variable measured. At large scale, estimated home ranges contained more open ground as northwestern gartersnake snout-vent-length (SVL) increased (presumably because they had fewer potential predators and could more afford to use open habitats). These results support my hypothesis that warm locations that are close to habitat edges

are important habitat for northwestern gartersnakes. The parks at which I conducted surveys appear to have large populations of northwestern gartersnakes with abundant habitat. However, the fact that habitat is used does not necessarily indicate that it is of high quality, and further research is required to determine if these populations are stable, increasing, or decreasing.

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Acknowledgments

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Dedication

I dedicate this thesis to the professors at Acadia University that created the block program, particularly Marty Snider, Soren Bondrup-Nielsen, Tom Herman, Don Stewart, and Dave Shutler. Through that program they taught me that the science of biology isn't simply a volume of facts I should struggle to memorize, but the fascinating, challenging, and creative process I love.

Chapter 1
General Introduction

Urban Parks as Wildlife Habitat

As the world's human population grows, urban areas are growing as well, and today more people live in cities than ever before (United Nations 2010). Urban parks can play an important role in the lives of those city dwellers who have little other contact with nature (Chiesura 2004). Although urban areas with high levels of anthropogenic disturbance may not support the diversity of wildlife present in more natural landscapes, numerous species can survive, and thrive, in urbanized environments (Mollov 2011). Therefore, urban parks are of value, not only to the people who visit them for recreation, but to wildlife that rely on parks to survive (Savard et al. 2000). The taxa supported by urban parks are diverse, including plants (Li et al. 2006), insects (Kitahara and Fujii 1997), birds (Fernandez-Juricic 2000), small mammals (Angold et al. 2006) and reptiles (Mollov 2005). The habitat requirements of each species vary, as does the level of anthropogenic disturbance they will tolerate (Ficetola et al. 2007). The design of urban parks and green spaces to promote wildlife habitat must consider which habitat characteristics are of greatest importance to the species in question (Angold et al. 2006).

Research in urban parks provides an opportunity to describe the habitat characteristics that are used by wildlife in these disturbed areas. This information can be used in conjunction with research on species in less disturbed areas to better understand the effects of urbanization on wildlife (e.g. Germaine and Wakeling 2001, Nagy and Rockwell 2013, Lövy and Riegert 2013). Reptiles and amphibians are in decline globally, and habitat loss has been identified as a major cause (Gibbon et al. 2000, Alford and Richards 1999). Studies of wildlife habitat use are important for conservation efforts because the habitat of a given species can be protected only after it has been identified. Also, studying the spatial ecology and habitat use of wildlife is necessary for managers and planners interested in maintaining wildlife populations within cities (Soulé 1991).

Objectives

The overall objectives of this study are to quantify the habitat used by northwestern gartersnakes (*Thamnophis ordinoides*) in city parks in Saanich, British

Columbia (in the Greater Victoria Area, 48˚27’33” N, 123˚22’36” W, Figure 1) and to determine how habitat where snakes are found differs from available habitat. These findings also should be useful for city park managers interested in maintaining populations of northwestern gartersnakes in wildlife sanctuaries and parks in Saanich, British Columbia, and throughout the range of this species.

I address the following specific questions:

- What are the main characteristics of habitats where snakes are found and how do they compare to those of habitat in general at the site?
- Does habitat use differ for snakes of different sex or physiological state (e.g. reproductive condition, feeding vs, non-feeding)?
- What patterns of habitat use at home range scale can be inferred from analysis of aerial photographs?

Study Sites

This study was conducted in the District of Saanich, part of the Greater Victoria Area, at the southern tip of Vancouver Island, British Columbia (Figure 1). Saanich has more than 150 urban parks and green spaces that range from open mowed sports fields to large patches of mature coniferous forest and vary in altitude from near sea level to 227 m (Saanich Parks and Recreation 2010). This study focused on five sites in Saanich where populations of northwestern gartersnakes were previously known to persist. Three of these sites, Mount Douglas, Layritz Park, and Mount Tolmie, are operated by the parks division of the District of Saanich, whereas the other two, Christmas Hill and Swan Lake, are operated by the Swan Lake/Christmas Hill Nature Sanctuary. Though all five sites allow daily public access, the activities allowed vary among sites. Mount Douglas and Mt. Tolmie also have roads that pass through portions of each park, and Layritz Park occasionally has municipal vehicles passing through. These parks and nature sanctuaries vary in size from 18.3 ha (Mt. Tolmie) to 181.6 ha (Mt. Douglas).

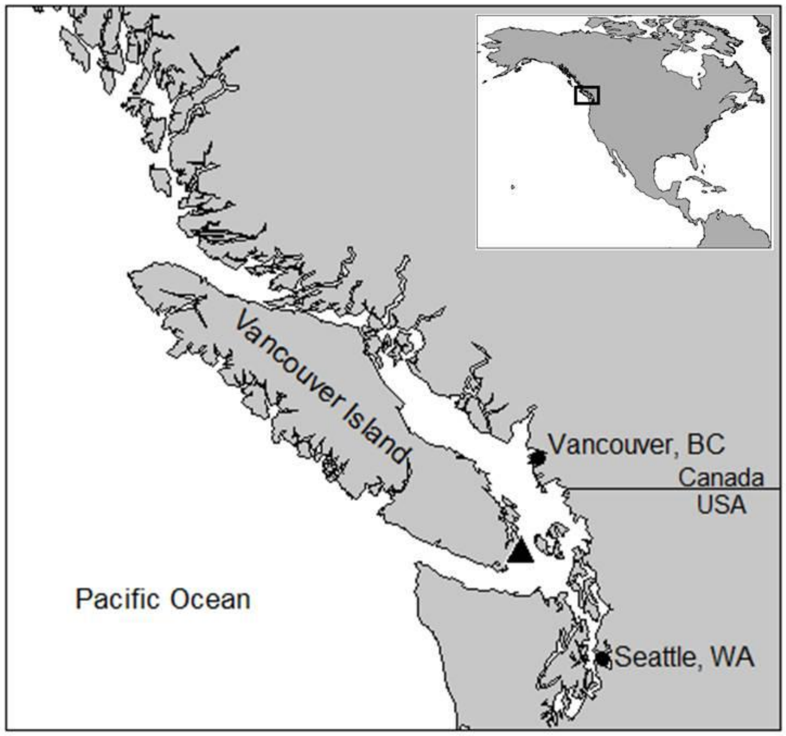

Figure 1. Map showing location of the Greater Victoria Area, British Columbia. The black box on the inset map of North America indicates the area enlarged. The black triangle is the location for the Greater Victoria Area, encompassing Victoria and Saanich. Created with data from Schute et al. (2013).

Study Species

The northwestern gartersnake, *Thamnophis ordinoides* (Baird and Girard 1852), is a small gartersnake found in western North America from northern California to coastal British Columbia, including Vancouver Island (Stebbins 2003). This species is common throughout much of its range and is often encountered by people (Matsuda et al. 2006).

On Vancouver Island, northwestern gartersnakes feed exclusively on slugs and earthworms (Gregory 1984). Northwestern gartersnakes also occasionally eat small amphibians and snails in some parts of their range (Brown et al. 1995, St. John 2002, Stebbins 2003). These snakes are reported to be associated with forest clearings, field margins, meadows, and open wooded areas (Gregory 1984, Stebbins 2003, Matsuda et al. 2006). Aside from these broad descriptions, however, a quantitative study of habitat use in this species has not been done. Northwestern gartersnakes at Spectacle Lake Provincial Park (48˚34’39” N, 123˚34’15” W) on Vancouver Island are non-migratory and use home-ranges (including hibernation sites) of approximately 0.178 ha on average, but ranging from 0.014 ha to 0.333 ha(Lawson 1991); however, these estimates are based on mark-recapture data, rather than more intensive radio-telemetry. In the Greater Victoria Area, northwestern gartersnakes are active from March to October (pers. obs.).

Variation between field sites

Having conducted this study at five separate sites across Saanich, it was necessary that I test for differences between sites to determine if it was reasonable to lump data collected at separate sites together in order to have a high sample size for statistical tests. Using principal components analysis (PCA) and Kruskal-Wallis tests I concluded that, overall, these sites are similar enough to justify lumping, and therefore all tests are performed using snakes captured across all five sites. Detailed description of the statistical methods used in this analysis, and test results, are in the appendix.

Chapter 2
Home on the edge: Edges are the most important structural habitat feature for northwestern gartersnakes

INTRODUCTION

City parks and green spaces provide refuge for species that would otherwise be absent in urban areas (Mollov 2011). Plants and animals that reside in these parks face challenges that are absent or diminished for their remote counterparts (Germaine and Wakeling 2001). In particular, urban parks often have high levels of disturbance from humans who use these parks for recreation. Despite such challenges, parks and green spaces provide habitat features that allow a wide diversity of species to survive (e.g. Helden and Leather 2004, Pattishall and Cundall 2009). Studying wildlife in urban and suburban areas is important to inform park managers and city planners who value the persistence of diversity within cities and wish to reduce human-wildlife conflict (DeStefano and DeGraaf 2003). To those ends, studies of the effects of urbanization on wildlife and of habitat use by wildlife within urban centres are useful (Soulé 1991).

Habitat use and habitat selection are both associated with the distribution of a given species (Thomas and Taylor 2006, Johnson 2007). They are related, but differ in that habitat selection is the process by which organisms establish patterns of habitat use (Reinert 1993). Studies describing patterns of habitat use are of interest both in their own right and as a first step for developing studies of habitat selection (Bastille-Rousseau et al. 2010). Broad qualitative descriptions of the habitat requirements for a species are useful starting points, but quantitative studies of small-scale habitat use are necessary for real utility to managers and ecologists.

For snakes, habitat structure, rather than plant species composition, is more important in differentiating between the habitats of two species (Reinert 1984a, 1984b). For example two populations of timber rattlesnakes (*Crotalus horridus*) occupied sites with little overlap in plant species composition, but nearly identical vegetative structure in terms of canopy cover and understory vegetation (Reinert 1993). Also, basking sites are of particular importance to reptiles as their digestive rate, speed of movement, foraging efficiency and reproductive success are all dependent on achieving optimal body temperature (Stevenson et al. 1985, Madsen 1987, Lutterschmidt and Reinert 1990, Elzer et al. 2013).

Previous studies of habitat selection in snakes found that milksnakes, *Lampropeltis triangulum* (Row and Blouin-Demers 2006), black ratsnakes, *Pantherophis obsoletus* (Blouin-Demers and Weatherhead 2001) and grasssnakes, *Natrix natrix* (Wisler et al. 2008) select habitat edges, likely to facilitate thermoregulation in close proximity to retreat sites. In particular, gravid females spend much of their time in areas of high thermal quality close to cover , such as fields, rocky outcrops and open areas (Huey et al. 1989, Charland and Gregory 1995, Row and Blouin-Demers 2006). Because of the importance of structural habitat features such as open basking sites, habitat edges, and canopy cover for thermoregulation and predator avoidance, I focus on quantifying habitat structure rather than identifying the species of plants that make up that structure.

Objectives

The objective of this study is to quantify the structural habitat features used by northwestern gartersnakes at parks in Saanich, British Columbia. To establish that an animal uses habitat non-randomly, the characteristics of locations where it has been found are compared to the characteristics of locations that are available to that animal but are not known to be used (Thomas and Taylor 2006, Johnson 2007). Following this method, I test for differences between locations where I found snakes and randomly chosen nearby locations. Habitat edges are important to northwestern gartersnakes (Stebbins 2003, Matsuda et al. 2006) and I predict that the same will be true in this study. Aside from describing how used habitat differs from available habitat for this species in general, I describe patterns of habitat use for snakes of different size class, reproductive condition and digestive state. I do so because some studies have found evidence for differential habitat use between large and small snakes (e.g. Blouin-Demers et al. 2007), differences in basking habits between mature and immature snakes (Webb and Whiting 2005), and that digestion or pregnancy will influence the thermal environment a snake will use (Gregory et al. 1999).

METHODS

Study Sites and Study Species

The northwestern gartersnake (*Thamnophis ordinoides*) ranges from northern California to southern British Columbia, and is found at low elevations throughout Vancouver Island. This species is smaller than many other gartersnakes (Rossman et al. 1996), and on Vancouver Island, eats exclusively slugs and worms (Gregory 1984). Northwestern gartersnakes are typically associated with forest clearings, field margins, and meadows (Gregory 1984, Stebbins 2003, Matsuda et al. 2006).

Saanich, British Columbia (48˚27’33” N, 123˚22’36” W) sits at the southern end of Vancouver Island (Figure 1), on the northern edge of Victoria, and these two cities form a continuous urban area. There are more than 150 parks and green spaces in Saanich, many of which hold populations of gartersnakes. I conducted this study at three parks and two nature sanctuaries that vary in habitat composition from mature Douglas-fir forest, Garry Oak woodland, fields, shrub-land, gravel trails, to roads and sports fields (Appendix).

Field Methods

With the help of a graduate student colleague, I conducted surveys from May to September 2012. Beginning in May, I conducted surveys along transects that were randomly determined in the field. To establish a random point to begin surveys I rolled an eight-sided die and walked between 50 and 400 paces into the study site along pre-existing trails. After pacing I spun the bezel of a compass to select a cardinal direction at random. I then followed that random transect, hand-capturing any snakes encountered. I completed a transect when I could no longer continue along a given bearing, either because I was at the edge of the park or encountered an impasse, such as a cliff or very dense thorny shrubs.

Beginning in June 2012, I incorporated habitat edges into snake surveys. I chose three vegetation height classes, 0 – 10 cm, 10 – 60 cm, and 60 cm or greater. I considered any boundary between two patches of vegetation of these classes to be an edge. Canopy cover, from trees or tall shrubs, could also form edges, resulting in six vegetation classes (each of the three height classes, with or without canopy cover). I began surveys as before, by selecting a random transect from a random point within the site. However, when I reached an edge between two vegetation height classes I ended that transect and began to survey the edge. While I followed the edge I used a 1.4 m pole divided into decimetres to measure vegetation and ensure I was following the edge. If the edge was formed around a closed patch of vegetation the original transect was resumed once the whole edge had been followed and I had returned to the location where I had begun the edge survey. For each edge survey I recorded the type of edge I was searching and the time in minutes that I spent searching it. In some instances an edge did not reconnect to the location where the transect had ended. This occurred usually because of a physical obstacle, such as a cliff or very dense thorny shrubs. On other occasions, an edge that was initially distinct became impossible to follow because the vegetation became patchy and of inconsistent heights. In either case, when I could no longer follow an edge, I once again spun the bezel of my compass and re-started a new random transect.

Any snakes encountered on transect or edge searches were captured by hand following Animal Care Committee Standard Operating Procedure # HP2002 (Capture, Handling, and Measurement of Non-Venomous Snakes in the Field). For each snake captured, I measured snout-vent-length (SVL), determined sex by probing for hemipenes (or by gently everting hemipenes in young males), palpated the stomach to determine if the snake had fed recently, and, if the snake was pregnant, palpated the abdomen to count embryos. I also recorded whether there were signs of any external injuries or ecdycis (cloudy eyes and/or venter) and measured the snake’s mass. Finally, I marked each snake with a passive-integrated transponder (PIT) tag to avoid using recaptures and thereby generating pseudoreplication in statistical analyses.

I recorded the UTM (NAD 83) and quantified the habitat surrounding capture locations, as well as a random paired location nearby, using 20 habitat characteristics (Table 1) that are of potential relevance to snakes (Reinert 1993, Blouin-Demers and Weatherhead 2001, Wisler et al. 2008).

Table 1. Habitat variables measured at each capture location and random point.

Variable Name	Description
Org. Litter	Proportion of organic litter in 1-m^2. Considered to be any organic litter; e.g. leaf litter, grass clippings, dead conifer needles.
Garbage	Proportion of garbage in 1-m^2. Recorded notes on type of garbage, i.e. size, material.
Herb. Veg.	Proportion of herbaceous vegetation less than 30 cm tall in 1-m^2. Considered to be any non-woody vegetation < 30 cm tall except moss.
Moss	Proportion of moss in 1-m^2. Recorded proportions of each species.
Woody Veg.	Proportion of woody vegetation less than 30 cm tall in 1-m^2. Recorded species.
Bedrock	Proportion of bedrock in 1-m^2.
Lg. Logs	Proportion of logs larger than 20 cm in 1-m^2.
Sticks	Proportion of sticks in 1-m^2
Sm. Rocks	Proportion of rocks smaller than 20 cm in 1-m^2.
Lg. Rocks	Proportion of rocks larger than 20 cm in 1-m^2.
Bare Soil	Proportion of bare soil in 1-m^2.
Stems	Number of woody stems in 1-m^2.
Canopy at Ground	Percent canopy cover measured from ground level. Measured with spherical densiometer.
Canopy at Waist	Percent canopy cover measured from waist height, 1 m from ground. Measured with spherical densiometer.
Slope	Slope of plot.
Aspect	Aspect at plot. Measured as degrees from zero
Dist. Edge	Distance from centre of plot to nearest habitat edge in metres. Edge defined as any edge formed between two patches of vegetation of height classes of interest.
Edge Type	Type of edge, based on vegetation height classes
Robel	1.4 m tall pole with alternating black and white dm segments. Measured as number of segments obscured by vegetation when pole placed at capture or paired location and viewed with eye level 1 m above ground and 3 m from pole. Measured at N, E, S, and W sides of plot.
Temp.	Substrate temperature (℃) at centre and 50 cm N, E, S, and W of plot
Litter Depth	Litter depth (cm) at centre and 50 cm N, E, S, and W of plot.

To determine the centre point for each paired-random plot I rolled an eight-sided die to select a compass bearing: 1 = North, 2 = North East, 3 = East, etc. I then walked 34 paces (approximately 50 m) in that direction. I chose 50 m as it is a distance that is within the possible range of movement for this species (Lawson 1991), so that the paired point represented a location that could potentially be used by that snake. To determine the middle point for the paired plot I walked 34 paces and placed a marker along the compass line. At each paired point I repeated all measurements taken at the capture point.

In some instances I encountered snakes but was unable to capture them. For these individuals I recorded the location in UTM (NAD 83) and, if I was certain that the species was *Thamnophis ordinoides*, I measured the habitat at the location where I encountered the snake and at a paired-random location.

I also recorded whether each capture took place on a transect search or edge search. I analysed edge and transect search effort using data from May 29 to September 8, 2012. I performed all data analyses using the programs R (R Core Team 2012) and Microsoft Excel (Microsoft 2007).

Habitat structure is generally suggested to be of greater importance to snakes than species of vegetation (Reinert 1993). To reflect this in data analysis I reorganized some habitat variables that I measured according to structure rather than taxonomy. For example, in the field I measured the total proportion of moss within each plot, but also recorded the proportion of those mosses that were taller and more structurally like herbaceous vegetation, and those that were short. A snake's ability to seek cover within the substrate is likely more important than the species comprising the substrate. I also combined habitat variables to create a category for large cover objects that included large rocks, large logs, and any piece of garbage that was similar to logs or rocks, e.g. construction materials. Finally I created a Bare Ground category that included all bedrock, bare soil, paving, gravel trails, and dead dry moss.

I ran analyses on all captures grouped as a whole (excluding recaptures to avoid pseudoreplication), and on subsets of snakes divided by sex, size class, and digestive state. I chose to combine all observations across all five field sites because no one site was distinct based on principal components analysis or Kruskal-Wallis tests (Appendix).

I approximated the point at which snakes in my sample were either mature or immature to divide my sample into two groups, one of larger snakes and one of smaller snakes. For females I assumed that snakes of approximately the same SVL or longer as the shortest gravid female were mature (larger size class). The smallest gravid female in this study was slightly larger than the smallest gravid female reported in the literature (Rossman et al. 1996). It was more difficult to determine a point at which to divide males, so to be consistent with females I chose a snout-vent-length that was slightly higher than the smallest mature male reported in the literature (Rossman et al. 1996). The point at which I considered snakes to be large or small only approximates the divide between sexual maturity and immaturity. However, for matched-pairs logistic regression, applied below, I could not include SVL in models, and therefore needed to define size classes to be able to fit models to subsets of individuals in those classes.

Univariate Analysis

I used R (R Core Team 2012) to test for differences between capture and random points one variable at a time. I use non-parametric Wilcoxon tests instead of parametric paired t-tests because data were non-normal (Shapiro-Wilks test). I compared capture and paired points for each variable using Wilcoxon signed rank tests. For each variable I also tested for differences between males, females, and gravid females.

Matched Pair Logistic Regression Modelling

Matched pair logistic regression is a form of logistic (i.e. binomial) regression modelling designed for use with paired data (Hosmer and Lemeshow 2000). This type of regression is more powerful for paired datasets than standard logistic regression because it focuses on differences between pairs of data collected together. In standard logistic regression it is assumed that each observation is independent (Manly et al. 2002). However, in a paired study, a random point is measured only if there is a capture to which it can be paired. As such, the number of random points is dependent upon the number of individuals captured. Therefore, although each pair is independent from each other pair, captures and paired points are not independent. By taking the difference between the values measured at capture and paired points one can form a dataset of differences, each of which is independent of all others. I subtracted the values measured at random locations from those at capture locations to obtain habitat differences and regressed those differences against a response of all "ones" (capture minus paired, or 1 – 0) with the intercept omitted (Hosmer and Lemeshow 2000). I selected variables for inclusion in a global model by fitting a univariate logistic regression model to obtain estimated coefficients and p values. I included any variable in the global model that had a p value < 0.25 (Row and Blouin-Demers 2006). Hosmer and Lemeshow (2000) suggest that using $p < 0.25$ is important to ensure that all variables of potential importance are included in the initial model.

Estimating the goodness of fit for a matched pair logistic regression model is difficult because methods that are typically used in standard logistic regression are not relevant to a model in which the response variable always has a value of one. Hosmer and Lemeshow (2000) recommend against using R^2 to determine goodness of fit in logistic regression because values are typically very low and a poor representation of the model's fit. Measuring the area under a receiver operating characteristic (ROC) curve can be used with standard logistic regression where one can compare the number of actual successes and failures to the number of times they are predicted by the model. However, in matched paired logistic regression, because the response variable is composed of all ones, this method cannot be used. Also, the Hosmer and Lemeshow test for goodness of fit is not applicable in matched pair logistic regression (Hosmer and Lemeshow 2000). Instead, I used bootstrapping to assess the overall fit of my best model using the function bootStrap, in the car package (Fox and Weisberg 2013). The bootstrap method is a process of internal validation that can be used for re-sampling many kinds of datasets (Westfall and Young 1993). Bootstrapping involves randomly sampling the original dataset, with replacement, to obtain new datasets which can then be used to recalculate the values of interest. Steyerberg et al (2001) reviewed several methods of internal validation for logistic regression models and found that standard bootstrap methods were best for establishing reliable estimates and standard errors. I ran 999 iterations and compared estimates and standard errors to those generated from my original model. I adapted the method in Steyerberg et al. (2001) and considered models to have a good fit if estimates and standard errors from bootstrapping overlapped the estimates and standard errors from model fitting.

Where the global model has an adequate fit, models fitted with the same dataset and a subset of those parameters will have a good fit as well (Mazerolle 2006). I used the function glmulti from the package glmulit (Calcagno 2013) to select candidate models. Glmulti is a package that performs automated model selection by fitting a model for every combination of variables in the global model and ranking the models by AICc values. I selected models as candidates if their AICc values were within 2 of the model with the lowest AICc. Burnham and Anderson (2002) suggest using AICc rather than AIC to select best models in any case where the ratio of sample size to number of model parameters (n/K) is less than 40. AICc is also useful because as sample size increases AICc values will approach AIC values (Mazerolle 2006). I calculated odds ratios and 95% confidence intervals based on parameter estimates and compared each model in the candidate set to all others in that set. Finally, after selecting my best model I fitted each variable that had previously been omitted to determine if the inclusion of any one of those variables significantly affected the model fit. I also removed each of the variables in best models one at a time, and tested for differences between models using likelihood ratio tests.

I fitted matched-pair logistic regression models for all northwestern gartersnakes captured and subsets of snakes that were postprandial, small, large, or gravid. It is more appropriate to use subsets based on size and reproductive condition than those based on sex because mature non-gravid females generally use similar habitat to males (Harvey and Weatherhead 2006), and immature snakes, which are generally smaller, use similar habitat regardless of sex (Blouin-Demers et al. 2007).

When fitting the model for postprandial snakes, I included the variable substrate temperature due to the well-established relationship between digestion and thermophily in reptiles (Gibson et al. 1989, Sievert 1989), regardless of the result of the univariate test.

RESULTS

Survey Efficiency and Population Structure

I collected habitat data at 133 capture points and 133 paired points. For nine of these 133 pairs I collected habitat data despite being unable to capture the snake. I captured 85 snakes on edge searches, 25 on transects, 18 snakes while walking into study sites or while relocating, and captured 5 snakes haphazardly (e.g. while walking to a paired plot or while eating lunch). I recaptured only three snakes and these recaptures were omitted from further analysis to avoid pseudoreplication.

I captured 124 northwestern gartersnakes, of which 67 were female (24 of which were gravid) and 55 male; I was unable to determine the sex of two individuals. I assume that males are mature at 240 mm SVL or greater. Therefore I captured 46 mature males and 9 immature males (Figure 2 A). The smallest SVL for a gravid female in my sample was 296.5 mm; for this study I assume that non-gravid females are sexually mature with an SVL of 290 mm or longer. Under this assumption, I captured 53 mature females and 14 that were immature (Figure 2 B).

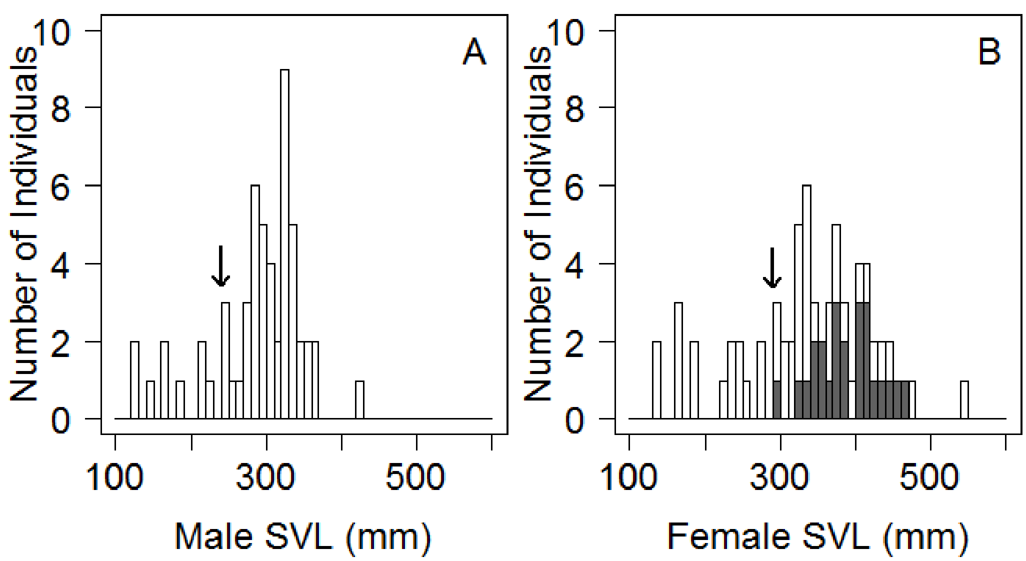

Figure 2. Histogram of snout-vent length (SVL) in millimetres, with intervals of 10 mm, for northwestern gartersnakes captured at all sites. A) males (n = 55), B) females (n = 67) grey bars indicate frequency of gravid females (n = 24). Arrow indicates division between large and small individuals used in univariate and regression analysis: 240 mm SVL for males, 290 mm SVL for females.

Univariate Analyses

I tested for differential habitat use between individuals of different sex and reproductive condition using Wilcoxon signed rank tests. Plots where I found male snakes had a greater proportion of herbaceous vegetation than random sites (Wilcoxon signed rank V=1957 p=0.006: Figure 3). The trend was similar for both nongravid and gravid females, but neither relationship was significant (V=947 p>0.5, V=305 p>0.5 respectively: Figure 3).

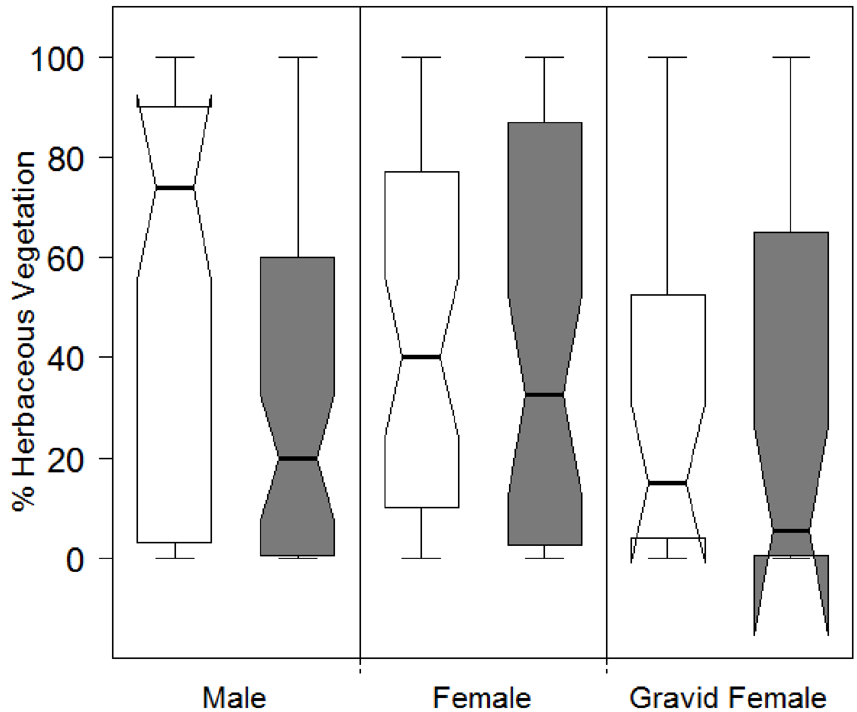

Figure 3. Boxplots of the proportion of herbaceous vegetation less than 30 cm tall in a 1-m^2 plot at capture (white) and random-paired (grey) locations for male, female, and gravid northwestern gartersnakes. The box represents the second and third quartiles while lines in the centre of each box represent the median, whiskers represent the first and fourth quartiles. Notches that do not overlap suggest significant differences.

I found nongravid female snakes at sites that had a greater proportion of organic litter than random sites (V=585.5 p=0.04: Figure 4). Gravid females followed a similar trend, but the difference was not significant (V=171 p>0.5). The trend was opposite for male snakes, but again the relationship was not significant (V=564 p>0.1: Figure 4).

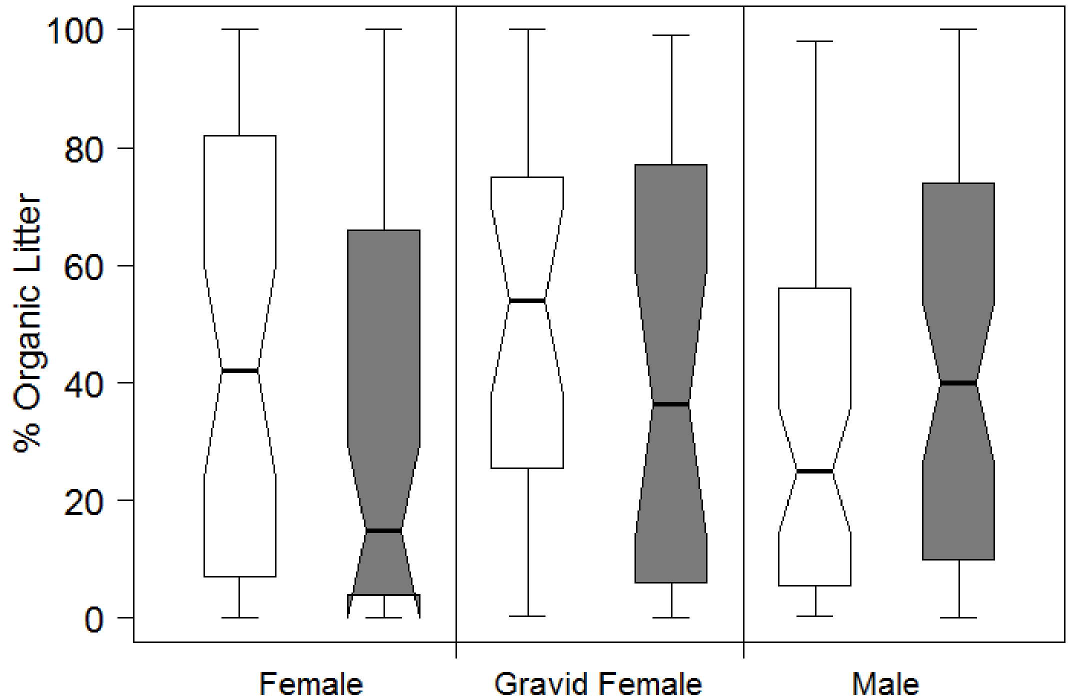

Figure 4. Boxplots of the proportion of organic litter in a 1-m^2 plot at capture (white) and random-paired (grey) locations for female, gravid female, and male northwestern gartersnakes. See explanation of boxplots in Figure 3.

As expected, the substrate temperature at locations where I found northwestern gartersnakes was significantly greater than the substrate temperature at paired-random locations (V=5359.5 p=0.02: Figure 5). However, this relationship approaches significance only for nongravid females (V=636 p=0.05) and is not significant for males or gravid females (gravid female: V=182 p=0.19, male: V=875 p=0.38).

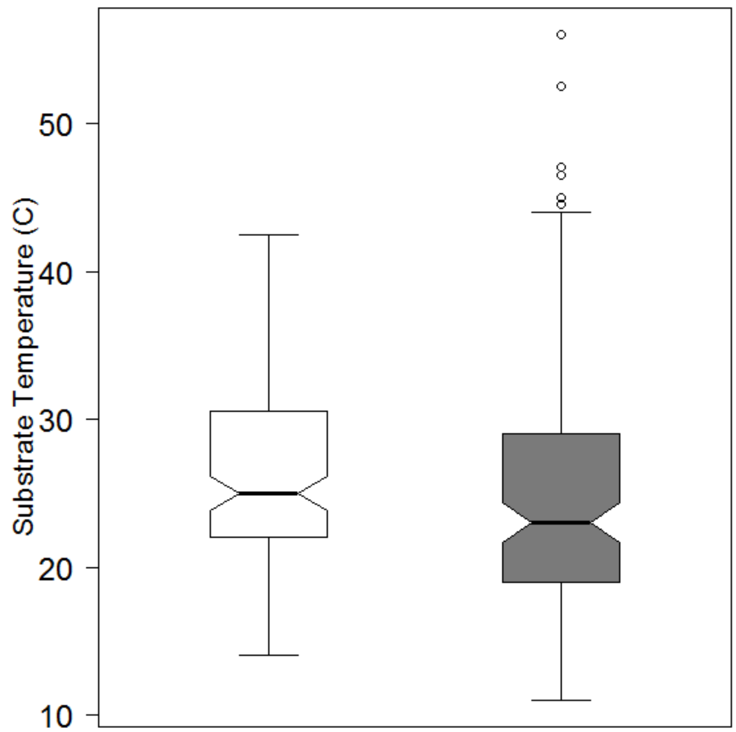

Figure 5. Boxplot of substrate temperature (C) measured at capture (white) and paired-random (grey) locations. Outliers are indicated as hollow circles; see explanation of boxplots in Figure 3.

The distance to the nearest habitat edge was lower at locations where I captured northwestern gartersnakes than the distance from random points to habitat edges (n = 133, V = 760.5, $p < 0.0001$: Figure 6 A). This relationship was maintained even after I removed all captures made during edge-focused surveys, n = 49, V = 165.5, p = 0.003 (Figure 6 B). Though I excluded edge surveys in Figure 6 B, it still includes plots from transect surveys and for snakes caught while pacing into a site, or pacing to relocate after reaching an impasse on a survey.

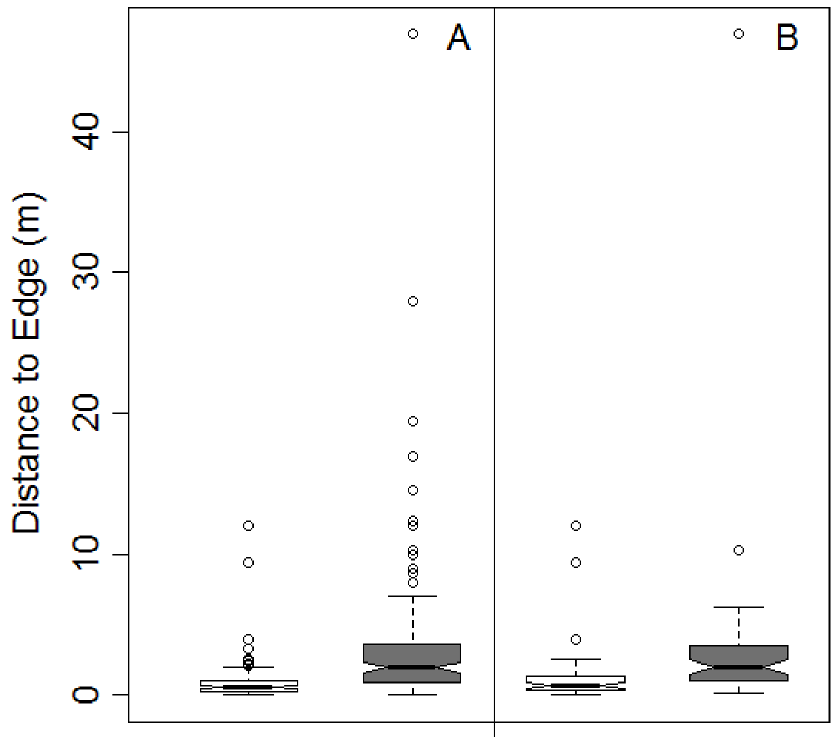

Figure 6. Boxplots of Distance to Edge (m) at snake capture plots (white) and random-paired plots (grey). A) All captures and paired-random plots. B) Captures and paired-random plots from edge searches removed. Outliers are indicated as hollow circles; see explanation of boxplots in Figure 3.

I also ran Wilcoxon signed rank tests for all other habitat variables measured at capture and paired plots, but these tests did not suggest there were significant differences and therefore I have omitted those results.

Matched-pair Logistic Regression Modelling

I fitted univariate matched-pair logistic regression models for each variable of interest and retained those variables with p-values less than 0.25 to be fitted in multivariate models. I fitted these univariate models using all northwestern gartersnakes captured, and subsets of large snakes, and postprandial snakes (Table 2). I also fitted models for small snakes (< 240 mm SVL for males, < 290 mm SVL for females), gravid females and snakes that showed signs of ecdycis. However, each of these models had relatively small sample sizes, each fewer than 30, and global models fit poorly. Due to their small sample sizes and poor model fit, I have excluded these models from further analysis. Results obtained by excluding each of these subsets of captures from the sample of all individuals were difficult to interpret and did not greatly influence model estimates or the variables that were included in best models.

Table 2. Variables for which univariate matched-pair logistic regression models were fitted and p-values for three datasets: all snakes captured, and subsets of large snakes (males > 240 mm SVL and females > 290 SVL), and snakes captured with food in their stomachs (postprandial). Variables for which p < 0.25 were included in global matched pair logistic regression models and are highlighted with *, and positive estimates are indicated with (+) and negative estimates with (-).

Variable	All Snakes	Large	Postprandial
Herb. Veg.	0.20 (+) *	0.22 (+) *	0.98 (-)
Cover Obj.	0.009 (+) *	0.008 (+) *	0.37 (+)
Bare Ground	0.005 (-) *	0.03 (-) *	0.32 (-)
Dist. Edge	< 0.0001 (-) *	0.002 (-) *	0.05 (-) *
Woody Veg.	0.36 (+)	0.34 (+)	0.14 (+) *
Sm. Rocks	0.42(+)	0.17 (+) *	0.90 (+)
Sticks	0.210(-) *	0.35 (-)	0.24 (-) *
Num. Woody Stem	0.70 (-)	0.63 (-)	0.07 (+) *
Temp.	0.24 (+) *	0.46 (+)	0.44 (+) *
Canopy	0.23 (+) *	0.24 (+) *	0.14 (+) *
Litter Depth	0.05 (-) *	0.23 (-) *	0.55 (-)
Robel	0.80 (-)	0.50 (-)	0.55 (+)
Slope	0.30 (+)	0.38 (+)	0.13 (+) *
Aspect	0.71 (-)	0.91 (+)	0.72 (-)

For all northwestern gartersnakes sampled, eight variables were significant at the < 0.25 level (Table 2). I first fitted a global model, with all variables of potential interest (Table 3), and tested the fit of this model by bootstrapping and comparing bootstrap estimates to model coefficients and standard errors (Table 4).

Table 3. Estimates, standard errors, z values and p values for global model fitted for all *T. ordinoides* captured. n = 110.

Variable	Coefficient	Std. Error	z value	Pr(>|z|)
Sticks	-0.023	0.035	-0.655	0.512
Canopy	0.004	0.006	0.691	0.489
Temp.	0.025	0.031	0.829	0.407
Litter Depth	-0.078	0.061	-1.295	0.195
Dist. Edge	-0.468	0.137	-3.432	0.001
Herb. Veg.	-0.001	0.007	-0.199	0.842
Cover Obj.	0.270	0.127	2.131	0.033
Bare Ground	-0.030	0.017	-1.784	0.074

Bootstrap estimates of model coefficients and their standard errors suggest a good model fit. Estimates and standard errors overlap for all variables and bias is low (Table 4). Given my assumption that the model fit was accurate, I fitted matched-pair logistic regression models for all possible combinations of the eight variables in the global model.

Table 4. Bootstrap estimates, bias, standard errors and medians from 999 iterations of a matched-pair logistic regression model fitted for all northwestern gartersnakes captured.

Variable	Estimate	Bias	Std. Error	Median
Sticks	-0.023	-0.012	0.115	-0.025
Canopy	0.004	-0.001	0.007	0.003
Temp.	0.025	-0.002	0.044	0.024
Litter Depth	-0.079	-0.014	0.100	-0.089
Dist. Edge	-0.468	-0.170	0.420	-0.521
Herb. Veg.	-0.001	-0.001	0.008	-0.002
Cover Obj.	0.270	0.523	2.511	0.299
Bare Ground	-0.030	-0.008	0.024	-0.034

Seven models (Table 5) had AICc values within two of the model with the best fit and I considered these models as candidate models (Burnham and Anderson 2002). Two variables, Distance to Edge and Cover Object were present in all seven candidate models and Bare Ground was present in all but the best model (Table 5). Litter Depth was present in three of seven candidate models while Temperature and % Sticks are each present in two candidate models (Table 5).

Table 5. Seven candidate matched pair logistic regression models, Log likelihood, K (number of parameters), AIC_c values, change in AIC_c and Akaike Weights.

Model	Log-likelihood	K	AIC_c	Δ AIC_c	Akaike Weight
Dist. Edge + Cover Object + Bare Ground	-47.84	3	101.90	0.000	0.221
Litter Depth + Dist. Edge + Cover Object + Bare Ground	-46.81	4	102.00	0.097	0.210
Temp. + Dist. Edge + Cover Object + Bare Ground	-47.23	4	102.83	0.927	0.139
Dist. Edge + Cover Object	-49.40	2	102.92	1.015	0.133
Temp. + Litter Depth + Dist. Edge + Cover Object + Bare Ground	-46.46	5	103.49	1.590	0.100
Sticks + Litter Depth + Dist. Edge + Cover Object + Bare Ground	-46.57	5	103.49	1.590	0.100
Sticks + Cover + Dist. Edge + Bare Ground	-47.58	4	103.54	1.639	0.097

Two variables, Distance to Edge and Cover Object have odds ratios and 95% CI that do not overlap one (Figure 7). The 95% CIs of the odds ratios for Litter Depth and Bare Ground slightly overlap one, and the 95% CIs for the odds ratios for Temperature and % Sticks both overlap one (Figure 7). An odds ratio that overlaps one indicates that an increase or decrease in that variable will not affect the probability of encountering a snake. The effect size of any one variable is not significantly different from one model to the next because their 95% CIs overlap between models (Figure 7). The variables Distance to Edge, Cover Object, and Bare Ground are all present in six of seven candidate models and I consider these as variables of greatest interest. The 95% CI of the odds ratio for Litter Depth has very little overlap with one, and therefore I consider this variable is important as well.

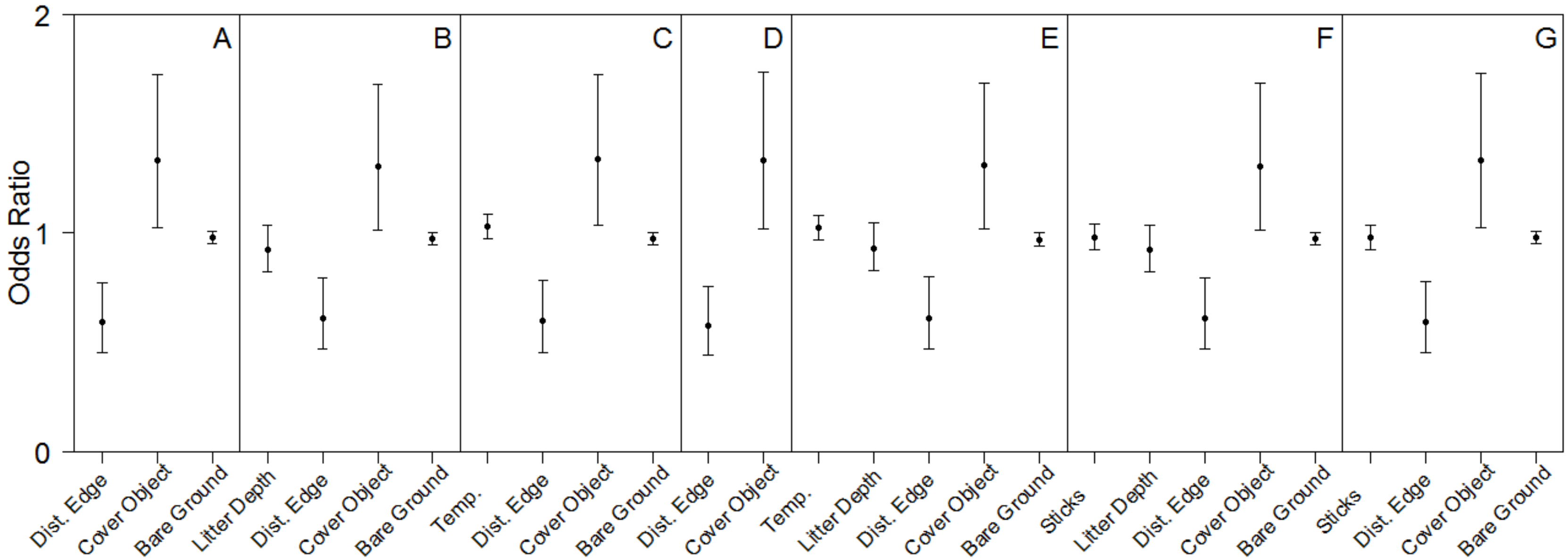

Figure 7. Odds ratios and 95% CI for variables present seven candidate models. An odds ratio greater than one indicates that an increase in the variable will increase the probability of encountering a northwestern gartersnake and an odds ratio below one indicates an increase in the variable will decrease the likelihood of encountering a northwestern gartersnake.

In matched-pair logistic regression, odds ratios are interpreted in a similar way as in standard logistic regression. A unit increase in the variable suggests a 1 +/- odds ratio change in the likelihood of the occurrence of the response (Hosmer and Lemeshow 2000). Therefore, the best candidate model suggests that a 1-m increase in the distance to edge will decrease the probability of encountering a northwestern gartersnake by 41 %, an increase by 1 % in the proportion of cover objects in a plot will increase the probability of encountering a northwestern gartersnake by 33 %, and an increase of 1 % in the proportion of bare ground will decrease the probability of encountering a northwestern gartersnake by 2 % (Table 6).

Table 6. Output from matched pair logistic regression with best fit for all northwestern gartersnakes sampled, AICc 101.90.

Variable	Estimate	Std. Error	z	p value	Odds	95%CI
Dist. Edge	-0.524	0.137	-3.818	0.0001	0.592	0.793,0.467
Cover Obj.	0.286	0.134	2.141	0.032	1.331	1.683,1.014
Bare Ground	-0.020	0.013	-1.507	0.132	0.980	1.003,0.944

Removing Distance to Edge or Cover Object and fitting models of the remaining two variables resulted in models that were significantly different, and whose AICc values were higher. Removing Distance to Edge had the greatest effect in reducing the fit of the model; the AICc increased from 101.90 to 134.91. Removing Bare Ground and fitting a model of Distance to Edge and Cover Object resulted in a model that was not significantly different (X^2 = 3.13, p = 0.077), but approaches significance.

To test for differential habitat use in different life stages I fitted matched-pair logistic regression models to subsets of my dataset. A subset of my dataset for non-gravid females with an SVL larger than 290 mm and males with an SVL larger than 240 mm left 75 paired observations for regression. Univariate tests indicated that I should include both Num. Woody Stems and proportion of woody vegetation and exclude the proportion of sticks (Table 2) for the global model (Table 7).

Table 7. Estimates, standard errors, z values, and p values for matched-pair logistic regression model fitted for large snakes (SVL > 240 mm for males, and SVL > 290 mm for females) excluding gravid females n = 75.

Variable	Estimate	Std. Error	z value	Pr(>|z|)
Small Rocks	-0.087	0.112	-0.772	0.440
Canopy	-0.001	0.011	-0.049	0.961
Litter Depth	-0.028	0.133	-0.213	0.831
Dist. Edge	-1.573	0.595	-2.643	0.008
Herb. Veg.	0.007	0.013	0.517	0.605
Cover Obj.	1.832	0.735	2.493	0.013
Bare Ground	-0.065	0.065	-0.993	0.321

Bootstrap estimates of model coefficients suggest an adequate fit; however the estimates of some coefficients are different from the original model coefficients and the bootstrap bias and standard errors were large (Table 8).

Table 8. Bootstrap estimates, bias, standard error and median of bootstrap estimates for 999 model iterations for all large snakes (SVL > 240 mm for males, and SVL > 290 mm for females) excluding gravid females.

Variable	Estimate	Bias	Std. Error	Median
Small Rocks	-0.030	-1.19E+12	1.14E+13	-0.002
Canopy	0.006	2.73E+10	7.69E+11	0.005
Litter Depth	0.08	-9.19E+11	1.13E+13	0.108
Dist. Edge	-0.487	-3.33E+12	2.78E+13	-0.587
Herb. Veg.	0.004	1.01E+11	1.13E+12	0.009
Cover Obj.	0.918	4.92E+12	4.41E+13	2.306
Bare Ground	-0.05	-2.71E+11	2.78E+12	-0.059

Best models, fitted for all large, non-gravid, individuals (Table 9) differed from those fitted with all captures in that litter depth was no longer present in all best models.

Table 9. Two best Matched-pair logistic regression models within 2 AICc values of best model of large northwestern gartersnakes (> 290mm SVL female, > 240mm SVL male). Parameters included in each model, log-likelihoods, AICcs and Akaike Weights.

Model	Log-likelihood	AICc	Δ AICc	Akaike Weight
Dist. Edge + Cover Object + Bare Ground	-13.04	32.51	0.00	0.5617
Small Rocks + Dist. Edge + Cover Object + Bare Ground	-12.79	34.30	1.798	0.2286

Each of the three candidate models within two AIC_c of the best model contain the variables Distance to Edge, % Cover Object, and % Bare Ground (Table 9). In all three models the 95% CI for these variables' odds ratios overlap, suggesting there is no significant difference between the size of the effect of those variables between each of the three candidate models (Figure 8).

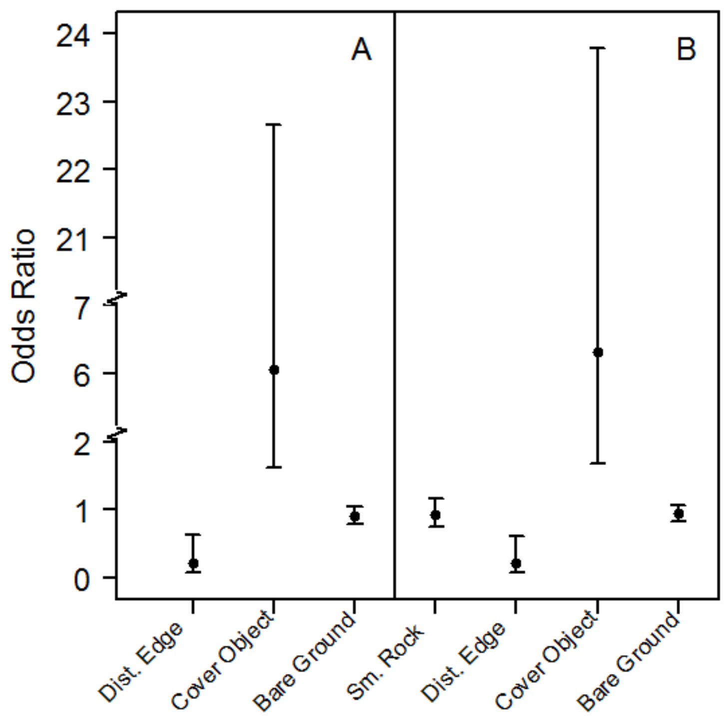

Figure 8. Odds ratios and 95% confidence intervals for two models, each within 2 AICc of best model, for northwestern gartersnakes captured with an SVL > 240 mm for males, > 290 mm for females, and excluding gravid females. Very large error around cover necessitated omitting sections of the y axis between 2 and 5, and 7 and 20.

Output from the best model for non-gravid, large northwestern gartersnakes suggests that % cover object influences the probability of detecting individuals. The 95% confidence interval is large, from 1.617 to 22.669, indicating a lack of certainty as to what degree the probability of encountering a snake will increase with an increase in % cover object, but there is still a strong likelihood that one will increase the other. Following the same trend as with the regression model for all individuals, an increase in the Distance to Edge decreased the probability of detecting an individual northwestern gartersnake. The odds ratio and 95% CI suggest that a 1-m increase in the Distance to Edge will decrease the probability of encountering a large, non-gravid, northwestern gartersnake by 78%, or between 92% and 40% (Table 10).

Table 10. Output from matched pair logistic regression for best model (AICc 32.51) for large northwestern gartersnake (> 240 mm SVL for males, > 290 mm SVL for females), also excluding gravid females.

Variable	Estimate	Std. Error	z value	p value	Odds	95% CI
Dist. Edge	-1.510	0.532	-2.837	0.00455	0.221	0.0778,0.627
Cover Object	1.801	0.674	2.673	0.00752	6.054	1.617, 22.669
Bare Ground	-0.0939	0.0712	-1.319	0.187	0.910	0.792, 1.046

Removing each of the three variables fitted to the best model for large northwestern gartersnakes one at a time resulted in models that were significantly different from the best model, and that had higher AICc values. Removing Distance to edge had the greatest effect, with the AICc value increasing from 32.51 to 70.13. Removing bare ground had the least effect, with the AICc increasing from 32.51 to 34.41; however a likelihood ratio test still suggested this model was different from the best model (X^2 = 4.16, p = 0.04). For snakes captured with food in their stomachs (n = 29), univariate tests indicated that I should include six variables in my global model. The global model retained seven variables (Table 11).

Table 11. Estimates, standard errors, z-values, and p-values for matched pair logistic regression model fitted for snakes captured with food in their stomachs n = 29.

Variable	Estimate	Std. Error	z value	Pr(>|z|)
Woody veg.	0.006	0.068	0.092	0.927
Sticks	-0.032	0.096	-0.327	0.743
Stems	0.100	0.119	0.838	0.402
Canopy	0.004	0.014	0.271	0.787
Slope	0.003	0.059	0.050	0.960
Dist. Edge	-0.318	0.199	-1.600	0.110
Temp	0.104	0.079	1.313	0.189

Bootstrap estimates did not differ from estimates from the initial model, but the bias and standard errors are large (Table 12). Therefore, though I am confident in the direction of the effect associated with each variable (either positive or negative), I am not confident in my ability to predict the magnitude of the effect.

Table 12. Bootstrap estimates, bias, standard error and median of bootstrap estimates for 999 model iterations for all snakes captured with food in their stomachs.

Variable	Estimate	Bias	Std. Error	Median
Woody veg.	0.006	5.38E+12	4.14E+13	0.040
Sticks	-0.032	-2.10E+12	1.09E+14	-0.077
Stems	0.100	3.90E+12	7.15E+13	0.094
Canopy	0.004	6.02E+11	5.08E+12	0.013
Slope	0.003	2.28E+12	1.69E+13	0.092
Dist. Edge	-0.318	-8.83E+12	4.70E+13	-2.848
Temp	0.104	3.98E+12	2.22E+13	0.194

For individuals captured with food in their stomachs the variables that contribute to best models are Number of Woody Stems, Distance to Edge and Substrate Temperature (Table 13). Of the eight best models, six retain Substrate Temperature as a variable of importance which suggests that Substrate Temperature is of greater importance to postprandial northwestern gartersnakes than it is to northwestern gartersnakes in general. Models fitted for postprandial snakes also suggest that those individuals use locations with more woody vegetation than others. Three of the four best models included the number of woody stems per plot, one contained the proportion of sticks, and the final model included the proportion of woody vegetation (Table 13).

Table 13. Four best matched pair logistic regression models, each within 2 AICc values of best model. Fitted with all postprandial snakes captured. Model parameters, log-likelihood, AICcs and Akaike Weights.

Model Parameters	Log-likelihood	K	AICc	Δ AICc	Akaike Weight
Woody Stems + Dist. Edge + Substrate Temp	-11.56	3	30.11	0	0.403
Woody Stems + Dist. Edge	-13.17	2	30.81	0.700	0.284
Sticks + Woody Stems + Dist. Edge	-12.50	3	32.01	1.90	0.156
Woody Veg. + Dist. Edge + Substrate Temp	-12.51	3	32.01	1.90	0.156

The three variables fitted in the best model (Table 13), Number of Woody Stems, Distance to Edge, and Substrate Temperature, are present in several of the three best models. Where those variables are present in other candidate models, the 95% confidence intervals around their odds ratios overlap (Figure 9). This overlap suggests that there is no significant difference between the size of the effect of each variable from one candidate model to the next.

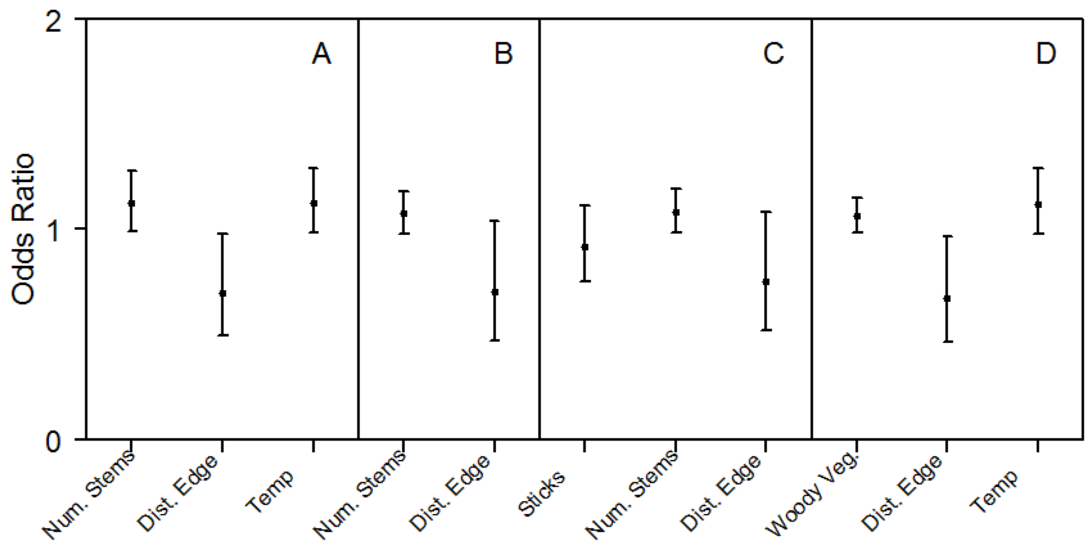

Figure 9. Odds ratios and 95% confidence intervals for four candidate models, each within 2 AICc of best model, for northwestern gartersnakes captured with food in their stomachs.

The best model of the set within 2 AICc values contains three variables: Woody Stems, Distance to Edge, and Substrate Temperature (Table 14). This model suggests that an increase in both the number of woody stems and substrate temperature will increase the probability of encountering snakes, and that a decrease in Distance to Edge will increase that probability (Table 14). An increase in the number of woody stems in a plot by one will increase the probability of encountering northwestern gartersnakes by 12%, with a 95% CI between -1% and 28%. Increasing the substrate temperature by 1 degree Celsius will increase the probability of use by northwestern gartersnakes with food in their stomachs by 13%, with a 95% CI between -2% and 29%. Finally, for snakes with food in their stomachs, an increase in Distance to Edge by 1 m will decrease the probability of use by 30%, with a 95% CI between -50% and -2%.

Table 14. Output from matched pair logistic regression for best model (AICc 30.11) for northwestern gartersnakes that were captured with food in their stomach.

Variable	Estimate	Std. Error	z value	p value	Odds	95% CI
Woody Stems	0.116	0.0650	1.783	0.0747	1.123	0.989, 1.275
Dist. Edge	-0.364	0.175	-2.080	0.0375	0.695	0.493, 0.979
Substrate Temp.	0.118	0.0695	1.693	0.0905	1.125	0.982, 1.288

I removed each variable from the best model for northwestern gartersnakes with food in their stomachs individually and tested for differences between models using likelihood ratio tests. Removing distance to edge or number of woody stems resulted in models that were significantly different from the best model ($X^2 = 8.23$, $p < 0.01$, and $X^2 = 5.50$ $p = 0.02$, respectively) and had AICc values that were higher, indicating a reduction in model fit. The difference between models with and without substrate temperature approaches significance ($X^2 = 3.22$ $p = 0.07$); however, the AICc was higher, which indicates a reduction in model fit.

DISCUSSION

Northwestern gartersnakes are regularly encountered on habitat edges (Gregory 1984, Stebbins 2003). Regardless of sex, reproductive condition, size, or digestive state, edges are the most important habitat feature for this species. Habitat edges are also used by many other species of snakes, including milksnakes, *Lampropeltis triangulum* (Row and Blouin-Demers 2006), and grasssnakes, *Natrix natrix* (Wisler et al. 2008).

Snakes use edges because they provide thermal gradients in close proximity to vegetative cover that can be a source of prey and, perhaps most important, provide escape from predators (Blouin-Demers and Weatherhead 2001). These gradients arise when forests are fragmented, creating edges that are generally warmer than the interior forest (Murcia 1995). It is likely that edges of fields, where I found northwestern gartersnakes, would maintain thermal gradients in much the same way as would a forest edge. Slugs in the genus *Arion* are more abundant in field edges than in fields (Eggenschwiler et al. 2013), providing prey for northwestern gartersnakes. Eastern massasauga rattlesnakes (*Sistrurus catenatus*) in Ontario (Harvey and Weatherhead 2006), and western gartersnakes (*Thamnophis elegans*) in New Mexico (Szaro et al. 1985) were regularly found near vegetative cover. I frequently saw potential predators at my study sites and it is thus not surprising that northwestern gartersnakes would be found near vegetative cover, either because those that spend too long in the open are eaten, or because these snakes are actually selecting positions near cover.

Aside from edges, cover objects, such as rocks, logs, and even trash are also used by many species of snakes. For example, broad-headed snakes in Australia are often found under rocks, and the illegal removal of rocks has been associated with a reduction in the abundance of that species throughout its range (Webb and Shine 1998). Cover from rocks also plays an important role in thermoregulation for western gartersnakes (Huey et al. 1989). Northern watersnakes (*Nerodia sipedon*) in Ontario were regularly found under rocks along a river (Gregory 2009). Large and small watersnakes were found using rocks as cover, with the exception of gravid females, which were generally found in the open (Gregory 2009). In my study, large rocks, logs, and other cover objects were not common at capture or random points, yet when they were present they were generally associated with northwestern gartersnakes. Some recreational areas in parks necessitate the removal of cover objects, such as sports fields; however, to maintain snake populations, managers should ensure that some portions of parks retain rocks and logs for cover.

The apparent use of sites with low litter depth is more difficult to interpret. In the southeastern United States, six species of small snakes had the highest relative abundance in areas of intermediate canopy cover and intermediate litter depth relative to areas of high canopy cover with deep litter, or clear cuts with no canopy cover and very little litter (Todd and Andrews 2008). One of these species, the northern redbelly snake (*Storeria occiptomaculata*), is found in similar habitats to those used by the northwestern gartersnake and also eats slugs and earthworms (Gilhen 1984, Semlitsch and Moran 1984). Also, grasssnakes in agricultural areas in Switzerland were found at sites with lower proportions of organic litter (Wisler et al. 2008). Perhaps shallow litter provides high thermal quality and cover that is not available from either deep litter, or where litter is absent, but further research is required to test this hypothesis.

Habitat use of gravid females often differs from that of males or non-gravid females (Reinert 1993, Charland and Gregory 1995). In many species of snakes, females do not eat while gravid, and focus on thermoregulation rather than foraging (Gregory et al. 1999). For example, gravid common gartersnakes (*Thamnophis sirtalis*) and western gartersnakes restrict their movements to areas of high thermal quality and males or non-gravid females move greater distances to forage (Charland and Gregory 1995). Thermophily in gravid females results in their use of more open habitats than males or non-gravid females (Madsen 1987). Males and non-gravid females may use vegetated areas to forage, although some snakes spend only approximately 2 % of their time foraging (Cundall and Pattishall 2011). In my study, males used higher proportions of herbaceous vegetation than available, and though the trend was the same, the relationship was non-significant for females and gravid females. The cause of these differences is unclear, but perhaps herbaceous vegetation plays a role as cover or a source of prey; short herbaceous vegetation could be used for basking.

It is well documented that reptiles are thermophilic while digesting food (Sievert 1989, Peterson et al. 1993, Gregory et al. 1999). For example, 90% of common gartersnakes in a laboratory setting used warmer shelters for the first day following feeding (Gibson et al. 1989). The mean substrate temperature at sites where I found snakes with food in their stomachs was 1.79℃ warmer than at sites where I found snakes without food. I also found postprandial northwestern gartersnakes at locations with higher numbers of woody stems than random locations. Slugs make up a large portion of the prey of northwestern gartersnakes (Gregory 1984) and it is possible that sites with more woody vegetation have higher moisture content and are better habitat for slugs. Huey et al. (1989) observed that western gartersnakes that had fed recently were more likely to remain in retreat sites (e.g. under rocks). Perhaps dense woody vegetation serves as cover while northwestern gartersnakes digest their food.

The low numbers of recaptures in this study made population estimation impossible, but suggest that populations are potentially large. The objective of this study was to describe habitat used by northwestern gartersnakes rather than to explain why these animals persist in urban parks. However, I speculate that their apparent abundance is partly due to Victoria's mild climate, which allows a long active season and an abundance of the invertebrates they eat. Northwestern gartersnakes consume both native and introduced slugs (Gregory 2013, pers. comm.). The native slug (*Ariolimax columbianus*) inhabits forests, whereas the introduced slug (*Arion ater*) inhabits forests, fields, shrubby areas and gardens (Rollo and Wellington 1975). The variety of habitats in which *A. ater* are found where *A. columbianus* are not suggests that prey availability may have increased for northwestern gartersnakes with the introduction of *A. ater*.

Despite this apparent availability of prey, the disturbance in urban parks may be influencing the size of northwestern gartersnakes. Lawson (1991) studied northwestern gartersnakes at Spectacle Lake Provincial Park, a site of similar size to some of Saanich's city parks (80 ha), but generally less disturbed. Snakes captured at sites in Saanich were generally smaller; the smallest gravid female sampled at Spectacle Lake had an SVL of 350 mm compared to 296 mm at my study sites. Also, a review of SVL at maturity found gravid northwestern gartersnakes were between 280 and 360 mm SVL (Rossman et al. 1996). Snakes in my study were sexually mature at the low end of this range which I speculate could be the result of the disturbances these snakes face in city parks because gartersnakes in highly variable environments elsewhere grow more slowly and are mature at smaller sizes (Bronikowski and Arnold 1999).

Unlike many other studies of habitat use by snakes (e.g. Harvey and Weatherhead 2006, Pattishall and Cundall 2009, Row et al. 2012), my study relied on visual encounter surveys, rather than radio-telemetry, and was therefore limited to a description of the habitat occupied by snakes that I could detect. One advantage of my approach is that I base my conclusions on habitat characteristics of locations that were used by many individuals, rather than the small samples of individuals typical of radio-telemetry studies (e.g. Harvey and Weatherhead 2006, Wisler et al. 2008, Shew et al. 2012). However, the strength of radio-telemetry is that it allows those few individuals to be re-located many times, even in places where they cannot be seen, thereby providing much more detail on actual habitat use than the 'snapshots' that I took. Unfortunately, except for the largest adult females, the small size of the snakes I studied precluded use of radio-telemetry and the approach I took may be the only one feasible for small snakes, which are generally understudied compared to larger species (e.g. Blouin-Demers et al. 2007). It is almost certain that northwestern gartersnakes use some habitat features in which I could never detect them, such as slash piles, or thorny thickets. Radio-telemetry of adult females would allow estimates of use of such habitat types. Even in large species of snakes, however, the ecology of small immature snakes is poorly understood and they may well use habitats differently from adults (e.g. cover: Webb and Whiting 2005). Coating snakes in fluorescent powder and tracking the trails left after they are released has been used to track individuals hundreds of metres (Furman et al. 2011), and could be used for tracking snakes that are too small for radio-telemetry over short time periods.

Ultimately, visual encounter surveys allowed me to obtain preliminary descriptions of patterns of habitat use for northwestern gartersnakes of different sexes and size classes; these findings represent hypotheses for future tests using different methods if and when available. Ideally, studies of habitat use for small snake species would incorporate visual encounter surveys, including inspection of cover objects, and radio-telemetry to address differential use for all size classes of that species.

CONCLUSION

Like most other animals, northwestern gartersnakes use habitat non-randomly. The habitat features at locations used by this species reflect its need for suitable basking sites that are in close proximity to vegetation or cover objects for escape. As in other species of snakes, northwestern gartersnakes use habitat differently when gravid or when they have recently consumed prey. Visual encounter surveys were sufficient to describe some qualities of the habitat used by this species, but not for patches of dense vegetation or other aspects of habitat where visual encounter surveys are difficult.

Chapter 3
The long and the short of it: Does body size influence the amount of open space in a snake's home range?

INTRODUCTION

It is unlikely that any species uses habitat randomly. Descriptions of non-random habitat use patterns are useful to wildlife managers who wish to maintain populations of species at risk or control introduced species (Blair 1996). The degree to which individuals of a given species favour particular habitat characteristics depends on factors such as their size (Byström et al. 2003), sex (Nikula et al. 2004), or time of year (Rueda et al. 2008). The relevant characteristics for describing habitat use vary depending on the scale being considered (Nikula et al. 2004) and including multiple scales can improve habitat use models (Altmoos and Henle 2010). However, determining which scale is appropriate requires careful consideration of the system being studied (Levin 1992). Large-scale habitat use studies often focus on home ranges, the areas that animals use for activities such as feeding, mating, and caring for young (Burt 1943). These studies describe habitat characteristics within home ranges and typically also investigate how those characteristics differ from unused habitat outside that animal's home range (Thomas and Taylor 2006).

Typically, an animal's home range is identified by repeated observations of that individual on the landscape, either through mark recapture or using radio telemetry (e.g. Nikula et al. 2004, Whitaker et al. 2007, Edworthy et al. 2012, Miller et al. 2012). These locations are used to estimate home ranges, typically by creating either minimum convex polygons (MCP) or kernel density estimates (KDE), though other methods are available (Laver and Kelly 2008). An MCP is the smallest convex polygon that includes all known locations for a given animal (Burgman and Fox 2003), whereas KDE uses the density of animal locations, giving more weight to areas that have been used more frequently, to create probability contours (Worton 1989). Though most studies use either MCP or KDE, some estimate home ranges using both methods because results can differ between the two (Laver and Kelly 2008). Whichever method is employed to estimate home ranges, interspecific and intraspecific variation in home-range size and shape is common. For example, home ranges can differ between individuals based on many factors such as sex (Whitaker et al. 2007, Livieri and Anderson 2012), body size (Blouin-Demers et al. 2007), reproductive condition (Thogmartin 2001), time of year (Beasley et al. 2007), latitude (Whitaker et al. 2007), and land use by humans (Shew et al. 2012, Lövy and Riegert 2013).

Once the size and shape of an animal's home-range has been estimated, habitat characteristics within that area can be identified. A home-range's spatial distribution is mapped in geographical information systems (GIS) and the habitat within is described, often using aerial photographs, satellite imagery, or other landcover data (e.g. Row et al. 2012, Miller et al. 2012, Lövy and Riegert 2013). Much like home-range size and shape, the habitat composition within a home range can vary by sex (Nikula et al. 2004), reproductive condition (Charland and Gregory 1995), or body size (Byström et al. 2003, Blouin-Demers et al. 2007); animals also use modified home ranges in response to disturbances, such as logging (Carey et al. 1990). The composition of an animal's home range reflects that animal's needs and must therefore contain both shelter and sources of food (Rasoma et al. 2013). Shelter is used for retreat from predators (Webb and Whiting 2005) and to escape potentially lethal temperature extremes (Webb and Shine 1998, Beck and Jennings 2003). Animals must also be able to acquire food within their home ranges (Bartlam-Brooks et al. 2013, Lövy and Riegert 2013); therefore home ranges must encompass habitat for the plants on which herbivores feed or prey for predatory animals.

In many species, home-range size and body size are associated, with larger animals having larger home ranges (Ottaviani et al. 2006). An animal's body size influences many of its interactions with other organisms. For example, body size affects predator-prey relationships (Kalinkat et al. 2013), where animals can seek shelter (Wahle 1992), and their diet (Luna et al. 2013). For an ectotherm, body size will also influence the rate at which its body temperature will fluctuate (Bittner et al. 2002).

Snakes have potential to serve as model organisms for studying relationships between home-range composition and body size because their morphology is consistent for individuals of different sex or age, but their body size is highly variable. Larger snakes are subject to a lower diversity of predators than small snakes (Mushinsky and Miller 1993) and large snakes modify their behaviour in response to this reduction in predation risk (Roth and Johnson 2004). Some snakes alter the composition of their home ranges as they grow larger, reflecting a change in predation risk and thermoregulatory needs (Blouin-Demers et al. 2007).

For many species, habitat use at certain life stages is more difficult to study than at others, and as a result some portions of animal's lives are poorly understood. This is particularly true of snakes, for which habitat relationships are most often studied using radio telemetry, but many young individuals (or small species) are too small to bear radiotransmitters. This lack of information for early life stages is detrimental to our understanding of those species as a whole. Studies that incorporate a gradient of body sizes, and consequently multiple life stages, are valuable to bridge this gap and improve understanding of habitat relationships for animals across their lifespan.

Studying home-range habitat composition without radio telemetry is difficult because snakes are cryptic and estimations of home ranges will lack precision without multiple relocations of individuals. However, in the absence of home-range size and shape estimates, putative home ranges could be assigned to locations where animals were located. If the size of these putative home ranges is based on the average home-range size estimated in past research on the species in question, they could perhaps serve for preliminary description of home-range composition for that species.

Objectives

In this chapter I address the relationship between a snake's size and the composition of its home range, under the assumption that all individuals in this study use home ranges of the same size and shape. Though it is unlikely that this is the case, this study is a preliminary attempt to describe patterns of habitat use at home-range scale for northwestern gartersnakes. I address the following questions:

- Can an average home-range size be applied to all individuals within my sample and used to describe patterns of habitat use?
- Does putative home-range habitat composition vary with body size for northwestern gartersnakes?

METHODS

Study Sites and Study Species

The northwestern gartersnake, *Thamnophis ordinoides*, is a relatively small snake that feeds on slugs and earthworms (Gregory 1984). This species ranges from northern California to southern British Columbia and is found at low elevations throughout Vancouver Island (Stebbins 2003). This species is associated with open woodlands, forest clearings and field margins (Gregory 1984, Stebbins 2003, Matsuda et al. 2006), though a detailed quantitative study of its habitat use has yet to be performed. City parks in Saanich, BC are composed of patches of forest and shrubs, grassy fields, and open areas without vegetation (e.g. bedrock, gravel trails, and parking lots; Appendix). The abundance of northwestern gartersnakes in city parks in Saanich, and the heterogeneity of habitat within these parks provide an ideal system within which to study habitat use of snakes in an urban area.

Field Methods

From May to September 2012 I surveyed five parks in Saanich for northwestern gartersnakes with the help of a graduate student colleague. I searched for snakes along random transects and habitat edges. I captured any snake encountered by hand following Animal Care Committee Standard Operating Procedure # HP2002 (Capture, Handling, and Measurement of Non-Venomous Snakes in the Field). For each snake captured, I recorded UTM (NAD 83), measured snout-vent-length (SVL), determined sex by probing for hemipenes (or by gently everting hemipenes in young males), palpated the stomach to determine if the snake had fed recently, and, if gravid, palpated the abdomen to count embryos. I also recorded whether there were signs of any external injuries, such as scars, exposed bone, or other wounds. Finally, I checked for signs of ecdycis (cloudy eyes and/or venter) and measured the snake’s mass.

Habitat Descriptions of Putative Home-Ranges

I collected habitat data at the home-range scale using air photos taken June 2011 and used geographical information system (GIS) to measure proportions of habitat types. I used the program QGIS (Quantum GIS Development Team 2013) for measuring air photos, and Microsoft Excel (Microsoft 2007) and R (R Core Team 2012) for statistical analyses.

Only one study has estimated home-range sizes for northwestern gartersnakes. Using mark-recapture, that study estimated that northwestern gartersnakes occupy home-ranges that are 1780 m^2, on average (Lawson 1991). In this study, I assume all individuals use home ranges of the same size and shape: a circle with an area of 1780 m^2 (23.8 m diameter) centred at the capture point recorded in the field. I measured the proportion within each circular home-range of three habitat types at a scale of 1:350 (Table 15). I used habitat characteristics that were sufficiently broad to be repeatable. Each circle had a total area of 1750 m^2, less than the actual area of a 23.8 m diameter circle because circles drawn in QGIS are circular polygons rather than perfect circles.

Table 15. Variables measured in home-range habitat composition analysis. Each measured as a proportion of 1750 m^2.

Variable	Description
Woody Veg.	Proportion of trees and shrubs in 1750 m^2.
Herb. Veg.	Proportion of herbaceous vegetation in 1750 m^2.
Without Veg.	Proportion of home-range without vegetation, such as bedrock, gravel trail, bare soil or paving.

Statistical Analyses

Quantile regression is used in cases where the dispersion of the conditional distribution of the response variable increases as a function of the predictor variable, resulting in a triangular distribution (Figure 10; Koenker and Hallock 2001). These situations arise where there appears to be some limiting factor but where there may also be other uncontrolled factors causing some individuals to fall below that limit (Thomson et al. 1996). For example, due to the fact that snakes swallow their prey whole, the maximum prey size for a snake is limited by that snake's size, and larger snakes can swallow larger prey (Shine 1991). However, some large snakes consume both large prey and small prey (Rodríguez-Robles 2002). Perhaps these large snakes eat smaller prey because small prey are more abundant, or easier to find. If prey abundance, or a snake's ability to detect prey, has not been measured then analyses cannot take these factors into account, and must focus on distributions of snake body size vs. prey size alone. These unmeasured factors, that cause some individuals to consume prey that are below the maximum prey size for their body size, will cause increased variance in prey size as body size increases, and result in wedge shaped distributions.

In the absence of data to explain why some individuals use a resource below the level to which they are limited, describing the upper edge of a distribution is useful. In these cases standard least-squares regression describing mean values will only poorly explain the relationship of interest (Koenker and Hallock 2001). However, approximate upper or lower boundaries of a such distribution can defined by quantile regression (Scharf et al. 1998, Cade et al. 1999).

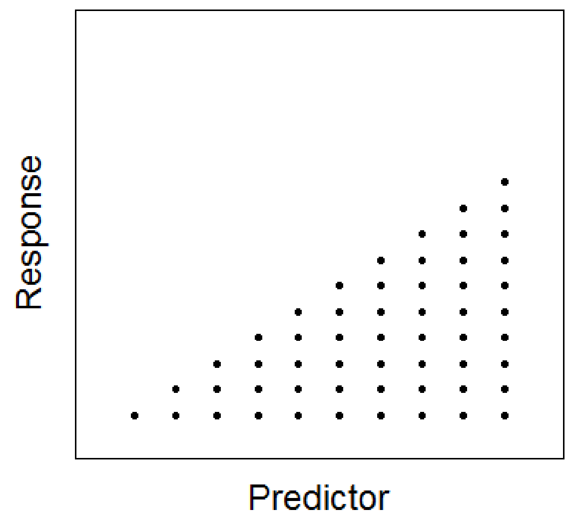

Figure 10. Scatterplot of generalized triangular distribution in which the variance of the response increases relative to the predictor.

I used the package quantreg (Koenker 2013) for quantile regression to examine the relationship between the proportions of each home-range scale habitat variable and northwester gartersnake's size (i.e. SVL and mass). Because it is difficult to define exact upper or lower limits, I fit quantile regression models for several possible limits. In particular, I considered the 90th and 95th percentiles as possible upper limits for distributions. Determining the highest quantile that can be estimated depends on the sample size and the distribution of the data (Cade et al. 1999). I tested for significance of quantiles by computing bootstrap standard errors and tested for differences between the slopes of these upper limits using the Wald approach (Koenker 2005).

I fitted regression quantiles for all snakes captured and to subsets of captures with gravid females removed, and for snakes that had signs of previous injuries. I removed gravid females because they often occupy home-ranges with higher proportions of unvegetated or lightly vegetated ground (Charland and Gregory 1995) and gravid females are generally larger (Shine 1994, Brown and Weatherhead 2000, Amarello et al. 2010), thus potentially confounding the effects of size and reproductive condition. Therefore, any apparent relationship between size and the proportion of open area in a snake's home range could be driven by gravid females. If a relationship between SVL and unvegetated ground exists, it should remain in the absence of gravid females.

I fit separate regression quantiles for snakes with signs of previous injuries because snakes that have been injured may modify their behaviour to avoid predation in the future (Gregory 2013). If having a home-range with larger unvegetated areas increases an individual's risk of predation, then those snakes that have been injured may use home ranges with smaller unvegetated areas.

RESULTS

I captured 124 northwestern gartersnakes, of which 67 were female (24 of which were gravid) and 55 male. I recaptured only three snakes, two of which were gravid females; the third was male. The gravid females moved only one and three m over periods of 18 and 22 days, whereas the male moved 40 m in 23 days. These recaptures were omitted from further analysis to avoid pseudoreplication.

Scatterplots of the proportions of woody or herbaceous vegetation within home-ranges have no clear relationships with the body metrics of the snakes using those home-ranges. However, as SVL increases the variation in the amount of a snake's home-range without vegetation also increases, resulting in wedge- shaped distributions (Figure 11 A). I fitted quantile regression models for the 90th and 95th percentiles of these distributions. Both have a positively sloped upper limit, are significant, and have confidence intervals that exclude zero (Table 16). Some large individuals used home-ranges with no unvegetated areas and therefore the lower limit of this distribution is a flat line at zero.

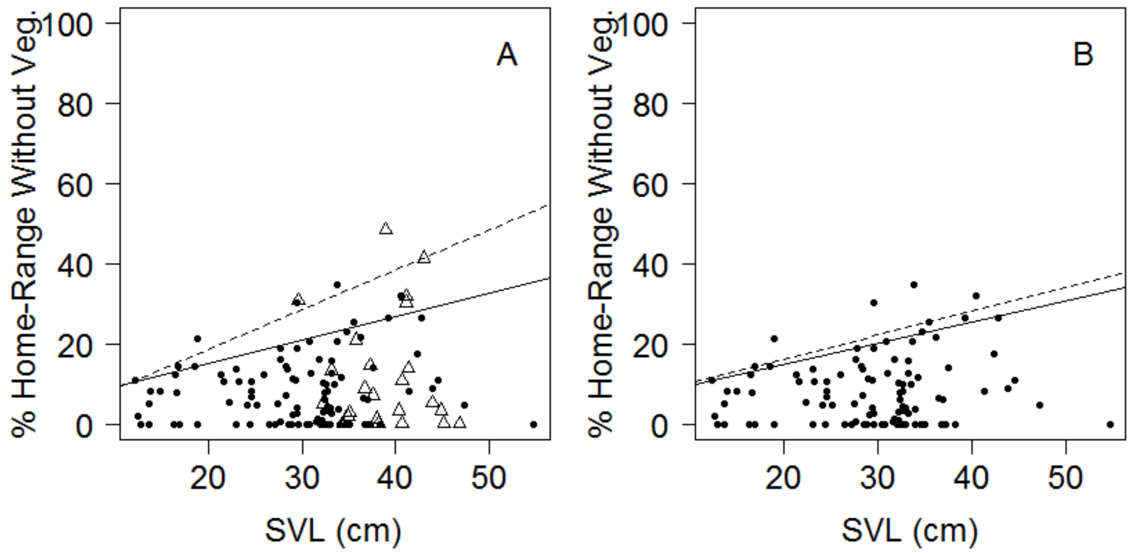

Figure 11. Scatterplots of northwestern gartersnake snout-vent-length (SVL) against the proportion of their home-range without vegetation. Lines represent regression for the 90th (solid line) and 95th (dash line) quantiles. A) All individuals captured (n = 124), dots are males and non-gravid females, hollow triangles are gravid females. B) Gravid females excluded (n = 24), dots are males and non-gravid females.

The difference between the slopes for the 90th and 95th percentiles approaches significance (Wald test F= 3.37, p = 0.07). Therefore, the relationship between SVL and the proportion of a snake's home-range without vegetation could be stronger at the 95th percentile than at the 90th (Figure 11 A). The slopes for models fitted to quantiles higher than 95th had confidence intervals that overlapped zero, and therefore have been omitted. Models for the 90th and 95th quantile fitted to observations with gravid females excluded remained significant (Figure 11 B).

Table 16. Slopes, confidence intervals, t-values and p-values for 90 and 95th quantile regression models for the proportion of a snake's home-range without vegetation against SVL for all individuals captured and with gravid females excluded.

	Percentile	Slope	Std. Error	CI	t-value	p-value
All Captures	95	0.995	0.241	0.332 - 1.108	4.122	0.0001
	90	0.588	0.163	0.491 - 0.811	3.611	0.0004
Gravid Excluded	95	0.595	0.237	0.251 - 0.748	2.514	0.0135
	90	0.523	0.153	0.381 - 0.640	3.422	0.0009

A scatterplot of SVL against the proportion of putative home-range without vegetation for northwestern gartersnakes with no signs of previous injuries maintains a ceiling distribution (Figure 12 A). However this relationship is not present for snakes with signs of previous injuries (Figure 12 B).

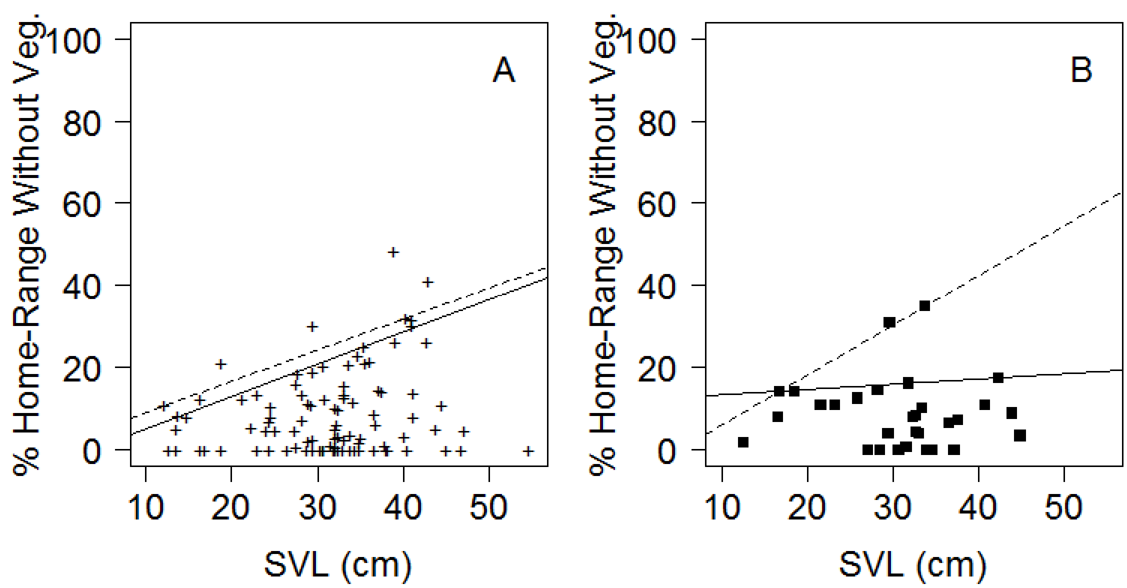

Figure 12. Scatterplots of northwestern gartersnake snout-vent-length (SVL) against the proportion of their home-range without vegetation. Lines represent regression for the 90th (solid line) and 95th (dash line) quantiles. A) Individuals without signs of previous injuries (n = 94). B) Individuals with signs of previous injuries (n = 31).

Regression at 90th and 95th quantile for uninjured snakes were significant (Table 17), but were not significantly different (Wald test: F = 0.018, p = 0.894). Regression at the 90th and 95th quantiles for snakes with signs of previous injuries were non-significant (Table 17), with slopes that cross and that are significantly different.

Table 17. Slopes, confidence intervals, t-values and p-values for 90 and 95th quantile regression models of the proportion of a snake's home-range without vegetation against SVL for northwestern gartersnakes with and without signs of previous injuries.

	Percentile	Slope	St. Error	CI	t-value	p-value
Uninjured	95	0.753	0.252	0.483 - 1.058	2.984	0.004
	90	0.787	0.184	0.562 - 0.869	4.264	0.0001
Injured	95	1.213	0.763	-2.298 - 1.346	1.589	0.123
	90	0.127	0.646	-1.165 - 0.884	0.197	0.846

Regression of the 90th and 95th quantile for snakes with signs of previous injuries have confidence intervals that overlap zero, indicating no relationship between SVL and the proportion of their home-ranges without vegetation. For snakes without signs of previous injuries the confidence intervals around the slopes do not overlap zero, and are significant, indicating there is a positive association between SVL and the proportion of unvegetated home-range for uninjured snakes.

DISCUSSION

This study assumes that all northwestern gartersnakes use home-ranges of the same size and shape. Though it is unlikely that this is true, and these results therefore should be interpreted with caution, in the absence of more accurate home range estimations for these snakes, putative home ranges are useful for preliminary description of habitat composition at this scale and for posing hypotheses for future test.

As northwestern gartersnakes grow longer, larger proportions of their putative home-ranges lack vegetation. However, there are still many large northwestern gartersnakes that occupy putative home-ranges with complete vegetative cover. The increase in the proportion of unvegetated areas in larger snake's home ranges is likely due to a trade-off between thermoregulatory benefits and predation risk. Gravid females in particular often use areas in which they are exposed for thermoregulation (Madsen 1987, Charland and Gregory 1995) and females are generally larger than males (Brown and Weatherhead 2000). That the relationship between SVL and the proportion of putative home-range lacking vegetation persists with gravid females removed provides strong evidence that this relationship is not being driven by large, basking, gravid females.

Birds are significant predators of snakes (Shine et al. 2001) and time spent in spaces without vegetation is presumably risky because snakes in such spaces are more visible from above. Snakes modify the degree to which they will risk predation based on many factors, including thermoregulation (Webb et al. 2009), feeding (Aubret et al. 2007), and for gravid females, embryonic development (Lorioux et al. 2013). Size is particularly important as large snakes face lower predation pressure (Shine et al. 2001) and fewer predator species than small ones (Mushinsky and Miller 1993). Longer snakes are more likely to show signs of previous injury than smaller snakes either because they are more likely to survive attacks or simply because they have had a longer lifespan over which to become injured (Gregory and Isaac 2005). Because of the benefits to being large, some snakes reduce anti-predator responses as they grow (Roth and Johnson 2004). Therefore, large snakes may use home-ranges with unvegetated areas because they are more likely to be ignored by predators, or because they can move more quickly to escape them (Kelley et al. 1997). Alternatively, larger snakes may have gained experience that will allow them to avoid predators, either by fleeing earlier when a predator approaches or avoiding high risk areas altogether. Snakes that survive attacks may gain experience from which they modify their behaviour to better avoid predators in the future (Gregory 2013). I found no relationship between SVL and the proportion of home ranges without vegetation for injured snakes. Therefore, snakes that have been injured in the past do not increase the proportion of unvegetated area in their home range as they grow bigger. This could occur if snakes that have been injured in the past are more wary than snakes that have not been injured, and continue to maintain home ranges with vegetative cover to avoid predators.

If my assumption is correct that areas without vegetation are riskier for snakes, there must be some benefit to occupying a home range that contains such areas. Northwestern gartersnakes feed on soft bodied invertebrates that desiccate easily (i.e. slugs and earthworms). Areas without vegetation, with the potential for greater solar radiation, could be risky for these prey and it is unlikely that snakes use unvegetated areas to forage. Instead, it is more likely that open areas provide thermal benefits to snakes that outweigh the cost of increased predation risk. Snakes bask in warm areas to digest food (Lutterschmidt and Reinert 1990), develop embryos (Madsen 1987), and increase metabolic rate (Peterson et al. 1993). Therefore, it is not surprising that northwestern gartersnakes use home-ranges that contain open areas. However, it is also possible that unvegetated areas, which are of high thermal quality for snakes in general may be of poor thermal quality for small snakes. Under the same thermal conditions, smaller snakes will reach their maximum body temperature faster than larger snakes (Bittner et al. 2002). Areas without vegetation, which become very warm on sunny days, could quickly become prohibitively hot for small snakes, even on moderately warm days. Vegetative cover may provide the moderate temperatures that small snakes require. Small snakes are often found under cover (Gregory 2009); however, tests of the thermal environment under cover suggested that small broad-headed snakes used cover despite it putting them at a thermal disadvantage (Webb and Whiting 2005). A combination of field and laboratory study would be useful to better understand this relationship. For example, temperature-sensitive PIT tags (e.g. Bittner et al. 2002, Gibbons and Andrews 2004) would be useful to determine body temperatures of small snakes in a variety of habitats, and using data loggers to record temperature fluctuations in open and vegetated areas could describe thermal gradients in habitats that are known to have been used by snakes.

All that said, some individuals use home-ranges that are mostly covered in vegetation. Despite the thermal benefits of open areas, snakes use vegetated areas for foraging (Shew et al. 2012), to evade predation (Szaro et al. 1985), and for shelter when air temperatures are higher or lower than optimal (Lelièvre et al. 2011). This is evident in the lack of individuals using home-ranges that were entirely composed of unvegetated ground. This is due in part to the rarity of such areas within my study sites, and because some areas with vegetation are likely essential to the survival of northwestern gartersnakes, particularly because their prey are likely more abundant in vegetated areas.

The lack of relationships with regard to other habitat variables measured at home-range scale (i.e. woody veg. or herbaceous veg.) is likely due to my use of very broad vegetative categories that are unlikely to represent how snakes use habitat. These home-ranges were also classified under the assumption that these snakes use circular home-ranges, which they are unlikely to do, and that snakes of all age, sex, or reproductive classes use home-ranges of similar size. For example, in many species of snakes, females use smaller home-ranges while gravid (e.g. Reinert and Zappalorti 1988, Charland and Gregory 1995). The three recaptures in this study suggest the putative home-ranges used here may be too large for gravid females and too small for males. In the time period between recaptures, gravid females moved across only a fraction of the putative home-ranges used here, while the male moved outside his putative home-range. The poor precision of these putative home-ranges is not surprising as their estimated size is based on mark-recapture of nine individuals, with great variation in home-range size, 140 m^2 to 3330 m^2 (Lawson 1991).

CONCLUSION

Using putative home-ranges I was able to describe some patterns of home-range habitat use for this species, and there does appear to be a relationship between a northwestern gartersnake’s body size and the composition of its home-range. However, the assumptions I made regarding the size and shape of those home-ranges limits my ability to interpret these results with certainty. Further research to increase the accuracy of home-range estimates for this species would ideally incorporate radio-telemetry or intensive mark-recapture to establish home-range estimates that are particular to each individual in a given study. Such studies would further understanding of the relationship between body size, home-range size, and habitat composition.

Chapter 4
Management Implications

Northwestern gartersnakes are abundant in city parks throughout the District of Saanich and the Greater Victoria Area. This species is well suited to persist within urban green spaces because it preys upon invertebrates, and regularly uses habitat edges, both of which are ubiquitous in urban parks.

The need to thermoregulate drives habitat use patterns for these animals and field edges provide temperature gradients which are vital for many aspects of their lives. The maintenance of trail systems and grassy fields for recreation provides edges that snakes will use provided that there also are vegetated areas in which snakes can forage and escape predators. Northwestern gartersnakes generally use edges between bare ground and herbaceous vegetation, but while they are digesting food they use areas with more woody stems. Therefore patches of herbaceous vegetation and shrubby areas should be maintained to meet the needs of snakes at different times. Also, that these snakes use organic litter as well suggests that perhaps leaving cuttings from landscaping may benefit snakes. Some species of snakes also use piles of branches for thermoregulation and leaving similar piles within urban parks could be beneficial to snakes in Victoria.

Cover objects, such as rocks and logs, are also important, particularly for small snakes. Rocks and logs are often removed from areas within parks that are designated for recreation, sports fields or trails, reducing cover availability for snakes. When cover objects are removed from recreational areas, rather than removing them from the park altogether, moving them to unmanicured areas within that park may help counteract their absence elsewhere.

As northwestern gartersnakes grow larger they may use home-ranges with higher proportions of unvegetated ground. These areas likely serve as basking sites for these large snakes. Large female snakes are demographically valuable as they have higher fecundity (Shine 1994), and promoting the habitat they use will presumably benefit the population as a whole. Increasing areas within home-ranges without vegetation increase the possibility that snakes will encounter predators and park visitors. For visitors, interpretive material would be beneficial to provide information regarding the value of snakes within urban parks. I did not collect detailed information regarding predator abundances, but personally observed parks visitors feeding crows multiple times. Supplemental feeding of crows appears to increase their abundance in parks, and crows are significant predators of snakes (Shine et al. 2001); educating park visitors about the problems associated with feeding wildlife would be beneficial.

In this study I was unable to estimate the size of the populations of snakes in Victoria's parks, though my lack of recaptures suggests these populations are large. However, the short-term nature of this study makes it impossible to determine whether these populations are increasing, decreasing, or stable. Future studies including mark-recapture over multiple years are necessary to determine the nature of population dynamics in urban parks in the Greater Victoria Area.

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Appendix
Park Descriptions

INTRODUCTION AND METHODS

To determine if it was reasonable to lump all northwestern gartersnakes captured at all five field sites I compared the values for all habitat variables measured at each park to one another. Detailed descriptions of each variable can be found in Table 1. I used R (R Core Team 2012) to run Principal Components Analysis (PCA), from the package Vegan, and Kruskal-Wallis tests. For PCA I used the function rda to generate eigenvectors and its associated plotting functions to generate biplots. PCA is not a statistical test (Borcard et al. 2011), but it is useful for exploring datasets and generating questions. Prior to PCA I tested for normality using Shapiro-Wilks tests (Royston 1982). I then transformed each habitat variable using arcsine transformations for proportion data and either log or square root transformations for all others. I used biplots to look for associations between capture or random points and habitat variables. I ran PCA with all observations, both capture and random, included in the same analysis. I looked for points grouping around certain habitat variables, based on whether they were capture or random points, from which field site they were, the sex and reproductive condition of the snake, and whether or not the snake was moving or still when I first observed it. I then used Kruskal-Wallis tests, a non-parametric equivalent to the one way ANOVA, to test for differences in individual variables across sites.

RESULTS

Thirty-one per cent of variation was explained by the first two principal components. Given this low proportion of variation explained, it is difficult to discern any strong trends; however biplots generated from PCA allowed for some description of differences in habitat between field sites. Along the axis for the first principal component, plots varied from high proportions of herbaceous vegetation to high proportions of organic litter, moss, and sticks (Figure 13). Across axis two, the greatest variation was due to the proportion of bedrock and higher substrate temperatures at one extreme, and higher robel measurements and greater litter depth at the other (Figure 13).

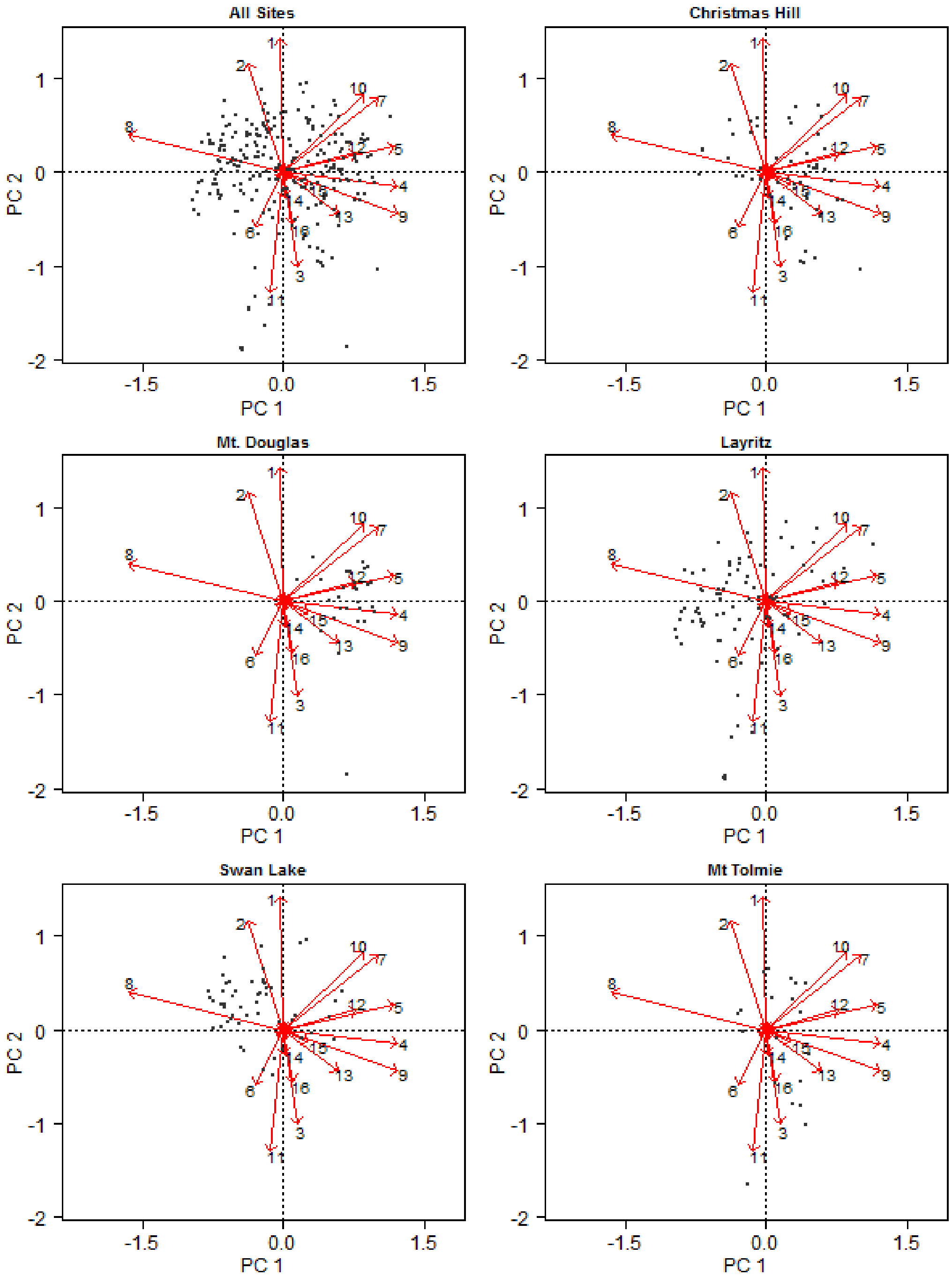

Figure 13. PCA biplots of principal components 1 and 2 for capture and paired plots for all sites, and for each site. Numbers represent habitat variables. 1 – Robel, 2 – Litter Depth at Centre, 3 – Temperature at Centre, 4 – Distance to Edge, 5 – Slope, 6 - % Organic Litter, 7 - % Canopy Closure, 8 - % Herb. Veg, 9 - % Moss, 10 - % Woody Veg., 11 - % Bedrock, 12 - % Sticks, 13 - % Cover Object, 14 - % Small Rocks, 15 - % Bare Soil, 16 - % Garbage

Plots from all sites overlapped, but those from Mt. Douglas Park were clustered more tightly than the other four sites, and had the least overlap with others (Figure 13). In particular, plots from Mt. Douglas Park and Swan Lake Nature Sanctuary showed very little overlap, suggesting these two parks had the greatest difference in habitat types (Figure 13).

Plots at Mt. Douglas clustered near % Sticks, % Organic Litter, Slope, and % Moss, and away from % Herb Vegetation. At Swan Lake, plots clustered away from Slope, % Organic Litter, and % Moss, and clustered near % Herb Vegetation and Litter depth. Kruskal-Wallis tests suggested that Mt. Douglas and Swan Lake differed significantly across all these variables (Figure 14). A Kruskal-Wallis test also indicated that Mt. Douglas generally had higher canopy cover than any other site, with only two observations near zero (Figure 14). Plots at Swan Lake had higher proportions of herbaceous vegetation and lower canopy cover (Figure 14).

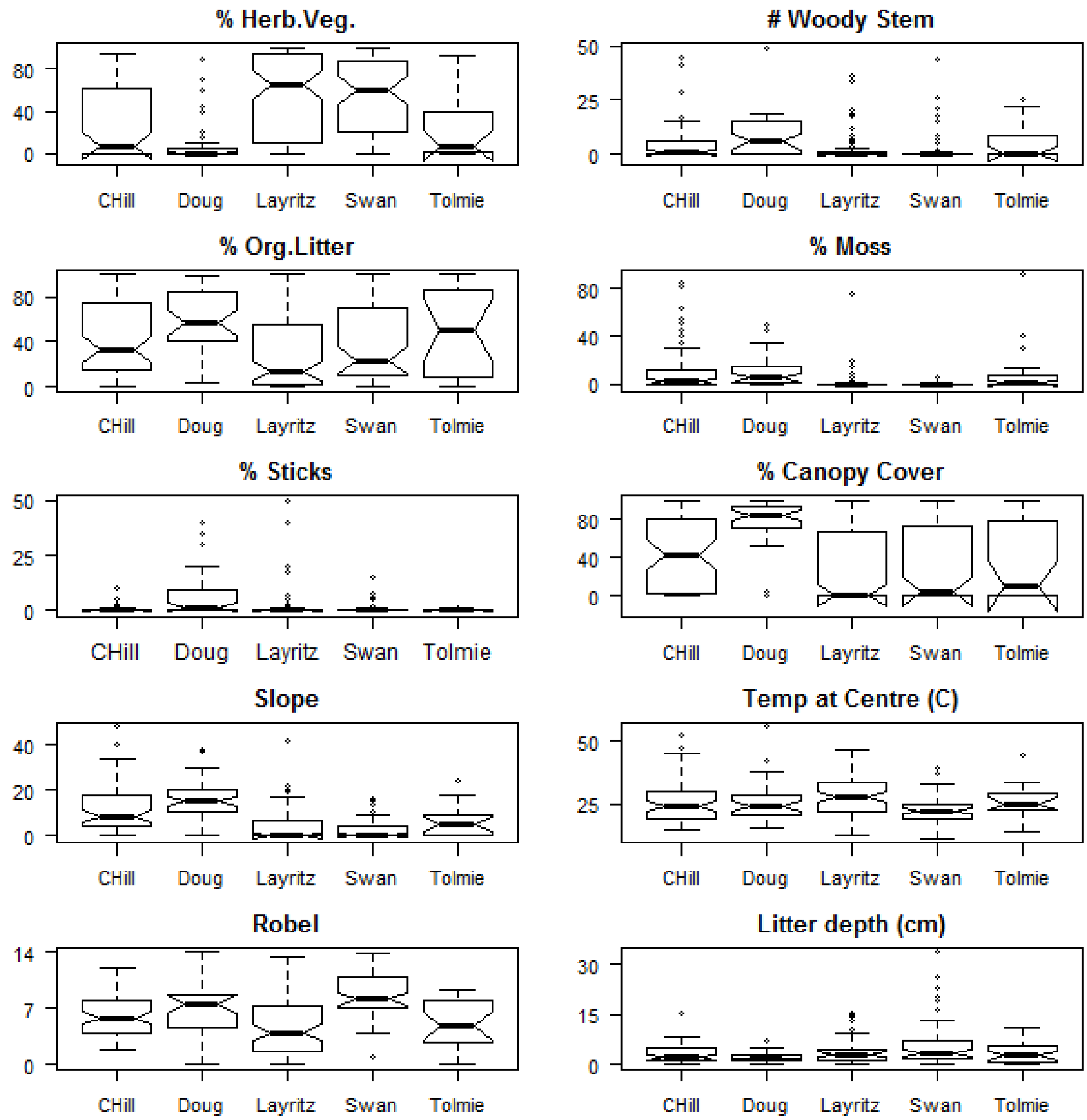

Figure 14. Boxplots of habitat variables, by site; Christmas Hill (Chill), Mt. Douglas (Doug), Layritz Park, Swan Lake (Swan), and Mt. Tolmie (Tolmie). Kruskal-Wallis tests suggest significant differences between sites. % Herb. Veg.; H = 57.44, df = 4, p < 0.001. # Woody Stem; H = 34.32, df = 4, p < 0.001. % Org. Litter; H = 28.57, df = 4, p < 0.001. % Moss; H = 118.05, df = 4, p < 0.001. % Sticks; H = 37.88, df = 4, p < 0.001. % Canopy Cover; H = 29.26, df = 4, p < 0.001. Slope; H = 75.52, df = 4, p < 0.001. Temp at Centre; H = 18.23, df = 4, p = 0.001. Robel; H = 53.86, df = 4, p < 0.001. Litter depth; H = 12.50, df = 4, p = 0.014.

Generally, habitat variables at the edges of the cloud of points for all sites (Figure 13) differed between sites based on Kruskal-Wallis tests (Figure 14) and habitat variables near the centre of the cloud of points did not differ significantly. All habitat variables that differed significantly between sites are presented as boxplots (Figure 14). Christmas Hill Nature Sanctuary overlapped with all four other sites, and had few plots at the extreme ends of either axis. Where Christmas Hill did differ significantly from other sites in Figure 14 it was generally intermediate between other sites (e.g. % Herb Veg. % Org. Litter, and % Canopy Cover), which supports the overlap in PCA (Figure 13). Layritz Park had plots that overlapped with Swan Lake, clustering nearer high % Herb Vegetation, but also had plots that clustered near % Bedrock. Again, Kruskal-Wallis tests supported this relationship (Figure 14), with both Layritz and Swan Lake having higher proportions of herbaceous vegetation. A Kruskal-Wallis test also suggested significant differences in proportion of bedrock between sites; however no site had many plots with bedrock. Mt. Tolmie had few observations overall, and had few observations that were not clustered tightly. Plots at Mt. Tolmie varied along the axis of PC2, between plots with high % Bedrock and high Robel values. Kruskal-Wallis tests suggested that Mt. Tolmie had lower proportions of herbaceous vegetation than Layritz Park or Swan Lake and a lower proportion of canopy cover than Mt. Douglas (Figure 14). Sites that had plots that spread more widely, such as Layritz, had the greatest diversity of habitat surveyed, whereas a small and tight cluster of points, such as Mt. Douglas, indicates a lower diversity of habitat.

CONCLUSION

Overall, these five sites are representative of the habitat types available on the Saanich Peninsula. Despite some differences in the habitats that were sampled, there is no one site that stands apart from all other sites across many variables. Therefore, I combined snakes captured across all five sites in all analyses.