

Edge-habitat Use by Northwestern Gartersnakes (*Thamnophis ordinoides*) in Saanich, British Columbia

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Understanding habitat requirements of species is fundamental for their conservation and urban parks can provide key habitat for species in otherwise disturbed settings. Northwestern Gartersnakes (*Thamnophis ordinoides*) are common in parks in Saanich, British Columbia, but their specific habitat requirements are poorly understood. Based on previous studies and thermoregulatory needs of snakes, we predicted that edges, particularly field margins, would be heavily used by active snakes. We therefore used surveys that focused on edges to find snakes and measured edge-habitat use by comparing habitat variables at locations where snakes were found to the same variables at nearby random locations. Habitat variables included composition and structure of vegetation, substrate temperature, aspect, and slope. Overall, litter depth, canopy cover, a lack of bare ground and woody vegetation were the most important habitat variables for determining where snakes were found. Our results provide a preliminary assessment to improve our understanding of habitat use for this species. The abundance of snakes found while surveying edges supports our initial assumption that edges are important habitat features but more work is required using multiple survey methods to further test this hypothesis.

Key Words: Northwestern Gartersnake; *Thamnophis ordinoides*; urban wildlife; reptiles; transect surveys; matched-pairs logistic regression; British Columbia

Introduction

City parks and green spaces provide refuge for species that would otherwise be absent in urban areas (Molloy 2011). Plants and animals that reside in parks face challenges that are absent or diminished for their counterparts in more pristine settings (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 can provide habitat features that allow a wide diversity of species to survive (Germaine and Wakeling 2001; Helden and Leather 2004; Pattishall and Cundall 2009). Studying wildlife in urban and suburban areas is important to inform park managers and city planners of the need to maintain diversity within cities and 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 habitats in which a species is found are useful starting points, but

quantitative studies of habitat use are necessary for real utility to managers and ecologists.

Habitat structure appears to be more important than plant species composition in determining habitat use of snakes. 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).

Many species of snakes use edge habitats preferentially for diverse purposes (Blouin-Demers and Weatherhead 2001a; Row and Blouin-Demers 2006). In Grasssnakes, *Natrix natrix*, which are related to garter-snakes, individuals select habitat edges presumably to facilitate thermoregulation in close proximity to retreat sites (Wisler *et al.* 2008; Reading and Jofré 2009). In particular, gravid female snakes 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, we focus on quantifying habitat structure

rather than identifying the species of plants that help make up that structure. Although such use of edges has not been tested for Northwestern Gartersnakes (*Thamnophis ordinoides* Baird and Girard 1852), much anecdotal evidence associates them with edges (Stewart 1968; Gregory 1984; Stebbins 2003). We therefore anticipated that edges would be commonly frequented by this species. In this study, we first used random surveys to determine that snakes were most easily detected in edge habitats and then restricted our further searches to edges so that we could determine the key features that distinguish these habitats from random points. We also restricted our analysis to active snakes (i.e., those detected in the open).

The objective of this study was to quantify the structural habitat features of edges used by active 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 approach, we tested for differences between locations where we found snakes and randomly chosen, nearby locations. We also compared patterns of habitat use for snakes of different sizes, reproductive condition, and digestive state, all factors previously shown to affect habitat use in snakes (Blouin-Demers and Weatherhead 2001a,b; Blouin-Demers *et al.* 2007).

Ideally, to study habitat use, we would use radio-telemetry to track snakes that would enable us to determine where snakes are even when they are hidden from view (Reinert and Cundall 1982; Weatherhead *et al.* 2012). Unfortunately, Northwestern Gartersnakes are relatively small snakes and not very suitable for radio-telemetric studies. However, they are abundant and often active in the open, where they can be readily seen and captured. Although we checked natural cover objects for snakes, we found virtually no snakes under cover. Despite the well-known utility of artificial cover objects in sampling snakes in many situations (Halliday and Blouin-Demers 2015), we did not use artificial cover objects in this study because we have not found them particularly effective in our previous work and because of problems associated with using them in public areas. Furthermore, it is arguable that factors determining habitat use by active snakes and by those seeking cover are separate issues (or at least only partially overlapping). Snakes use cover non-randomly and particular features of cover objects seem to be important in determining their use by snakes. Thus, this study addresses only one small element of the complexities of habitat use by Northwestern Gartersnakes by determining patterns of habitat use of active snakes only. Also, visual encounter surveys of active snakes are limited in that we can only sample snakes that we are able to detect and capture. The results therefore comprise a working hypothesis for future study using appropriate long-term tracking technology when it becomes available.

Study Area

Saanich, British Columbia (48.459°N, 123.377°W) sits at the southern end of Vancouver Island, on the northern edge of Victoria, and these two cities form a continuous urban area. We conducted this study at three parks, Mount Douglas, Mount Tolmie, and Layritz, and two nature sanctuaries, Christmas Hill and Swan Lake. These sites vary in habitat composition from mature Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*) forest, Garry Oak (*Quercus garryana* Douglas ex Hooker var. *garryana*) woodland, fields, shrub-land, gravel trails, to roads and sports fields.

Methods

We conducted surveys from May to September 2012. We alternated visiting each site to spend an equal number of days surveying each and to survey evenly across the field season. We focused our surveys between 1000 h and 1600 h and all surveys were conducted by the same two observers, walking at a consistent pace, with one in front of the other. We also searched under every cover object encountered within 1 m either side of the survey route. Beginning in May, we conducted surveys along transects that were randomly determined in the field by spinning the bezel of a compass. Beginning in June, we incorporated habitat edges into snake surveys to increase the number of snake encounters. We chose three vegetation height classes, 0 – 10 cm, 10 – 60 cm, and >60 cm. We 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). Edge surveys consisted of two observers walking at a consistent pace along the boundary between these two vegetation height classes. The boundaries between these vegetation height classes were created by vegetation management (e.g., mowing) and/or occurred naturally (e.g., around patches of bedrock).

We began surveys by rolling an eight-sided die to determine the number of paces to walk into a site. Once we had reached the end of a given number of paces we spun the bezel of a compass to select a random transect to follow. When we reached an edge between two vegetation height classes we ended that transect and began to survey 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 we had returned to the location where we had begun the edge survey. For each edge survey we recorded the type of edge we were searching, and the time in minutes that we spent searching it. In some instances, an edge did not reconnect to the location where we ended the transect. This usually occurred 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

we could no longer follow an edge, we spun the bezel of a compass to determine the direction of a new random transect. Therefore, each individual survey, a combination of transects and edge searches, was of indeterminate length. We ensured consistent search effort by always walking at a consistent pace and spending an equal number of days searching each site.

We captured snakes by hand, and for each we measured snout-vent-length (SVL), determined sex by probing for hemipenes (or by gently evert hemipenes in young males), gently palpated the stomach to determine if the snake had fed recently, and palpated the abdomen of mature females to determine reproductive status (pregnant or not). Finally, we marked each snake with a passive-integrated transponder (PIT) tag (Avid encrypted 125 kHz, Avid Identification Systems, Norco, California, USA) to avoid including recaptures in statistical analyses and thereby generating pseudoreplication (Hurlbert 1984).

We quantified the habitat surrounding capture locations, as well as a random paired location nearby, using 13 habitat characteristics (Table 1) that are of potential relevance to snakes (Reinert 1993; Blouin-Demers and Weatherhead 2001a; Wisler *et al.* 2008). Habitat variables were measured at capture locations immediately after each snake was captured. Habitat variables were measured at paired locations immediately after completion of the measurements at capture locations, typically within 20 min.

To determine the centre point for each paired-random plot we rolled an eight-sided die to select a compass bearing: 1 = North, 2 = Northeast, 3 = East, etc. and then walked about 50 m in that direction (measured by pacing). We chose 50 m as a distance that is within the potential movement range of an individual Northwestern Gartersnake in a day (Lawson 1991), but large enough to capture habitat heterogeneity. To determine the middle point for the paired plot we walked 50 m and placed a marker along the compass line. At each

paired point we repeated all measurements taken at the capture point.

In some instances we encountered snakes but were unable to capture them. If we were certain that the species was Northwestern Gartersnake, we measured the habitat at the location where we encountered the snake and at a paired-random location.

We also recorded whether each capture took place on a transect search to determine the relative frequency that snakes were found on edges, or edge search to determine what characteristics of edges were important. We analysed edge and transect search effort using data from 29 May to 8 September 2012. We performed all data analyses using R (R Core Team 2012).

We tested all variables for normality using Shapiro-Wilks tests and assessed the correlation of each possible pair of variables. We ran analyses on all captures grouped as a whole and on subsets of snakes divided by survey type, sex, size class, and digestive state. We omitted recaptures due to small sample size ($n = 3$) and we also excluded all individuals found under cover objects because we found relatively few of them ($n = 7$) and therefore focused our study on active snakes. We 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 (Dixon-MacCallum 2013). For matched-pairs logistic regression, described below, we 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.

Because our data were non-normal, we used a non-parametric Wilcoxon sign-rank test, instead of a parametric paired *t*-test, to compare the distance from each capture point to the nearest habitat edge and the distance from each random point to the nearest habitat edge. We first performed this test using all captures, regardless of survey type. We then retested after removing all individuals captured on edge surveys. We also

TABLE 1. Habitat variables measured at each Northwestern Gartersnake (*Thamnophis ordinoides*) capture location and associated random point and *P*-values for univariate matched-pair logistic regression models for snakes captured while surveying edges ($n = 84$). Variables for which $P < 0.25$ were included in a global matched pair logistic regression model and are highlighted with *; positive estimates are indicated with (+) and negative estimates with (-).

Variable	Description	All snakes
HerbVeg	Herbaceous vegetation < 30 cm tall (% of 1 m ²)	0.070 (+)*
WoodyVeg	Woody vegetation < 30 cm tall (% of 1 m ²)	0.100 (+)*
CoverObj	Logs, rocks, or garbage > 20 cm (% of 1 m ²)	0.090 (+)*
Sticks	Sticks (% of 1 m ²)	0.450 (-)
SmRocks	Rocks < 20 cm (% of 1 m ²)	0.520 (+)
BareGround	Bare substrate or moss (% of 1 m ²)	0.010 (-)*
Stems	Number of woody stems in 1 m ²	0.880 (+)
Canopy	Canopy cover (%), measured 1 m from ground with spherical densiometer	0.090 (+)*
Slope	Slope of plot	0.700 (+)
Aspect	Aspect at plot (° from 0)	0.490 (-)
DistEdge	Distance from centre of plot to nearest habitat edge (m)	0.001 (-)
Temp	Substrate temperature (°C)	0.650 (+)
LitterDepth	Litter depth (cm)	0.040 (-)*

conducted an ANCOVA to test the effect of habitat type (i.e., forest or field) on snake captures with search time as a covariate.

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. We 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). We selected variables for inclusion in a global model by fitting a univariate logistic regression model to obtain estimated coefficients and P values. We 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 $P < 0.25$ ensures that all variables of potential importance are included in the initial model. We fitted these univariate models using all Northwestern Gartersnakes captured excluding those captured on transects and those found under cover objects (Table 1). We also fitted models for large snakes, small snakes, gravid females, and postprandial snakes. However, each of these models was based on relatively small samples, each fewer than 30, and global models fit poorly; we therefore excluded these models from further analysis.

Typically, model selection is performed by choosing a set of candidate models *a priori*, then fitting each model and comparing output to choose best models and models for averaging (Mazerolle 2006). Our method differs in that we developed our set of candidate models by fitting all possible combinations of variables selected by the method described above. We followed this method because we hypothesized that all the variables we measured (Table 1) could potentially play some role in habitat use for this species. Therefore, we were interested in determining which combination of those variables could best describe habitat use for this species.

We used bootstrapping to assess the overall fit of our models using the function *Boot*, in the package *car* (Fox and Weisberg 2011). Bootstrapping 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 that 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. We ran 999 iterations and compared estimates and standard errors to those generated from our original model. We 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. We fitted a global model, with all variables of potential interest and tested the fit of this model by bootstrapping and comparing bootstrap estimates to model coefficients and standard errors. Bootstrap estimates of model coefficients and their standard errors suggested a good model fit. Estimates and standard errors overlapped for all variables and bias was low.

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). We used the function *glmulti* from the R package *glmulti* (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 AIC_c values. Models within 2 AIC_c (i.e., ΔAIC_c 0–2) of the best model have substantial support, those with a ΔAIC_c of 4–7 have considerably less support, and those with a $\Delta AIC_c > 10$ have essentially no support (Burnham and Anderson 2002: 70). We considered all models with $\Delta AIC_c < 7$ and selected models with $\Delta AIC_c < 2$ for model averaging. We conducted model averaging to determine parameter estimates and standard errors following Burnham and Anderson (2002). We fitted matched-pair logistic regression models for all Northwestern Gartersnakes captured on habitat edges.

Results

We collected habitat data at 130 capture points and 130 paired points. For nine of these 130 pairs we collected habitat data despite being unable to capture the snake. We captured 84 snakes on edge searches, 25 on transects, 16 snakes while walking into study sites or while relocating, and captured five snakes haphazardly (e.g., while walking to a paired plot). We recaptured only three snakes and these recaptures were omitted from further analysis.

Capture sites were closer to the nearest habitat edge than were random sites ($n = 130$, $W = 760.5$, $P < 0.0001$; Figure 1A). This relationship was maintained even after we removed all captures made during edge focused survey ($n = 46$, $W = 165.5$, $P = 0.003$; Figure 1B). Of the 84 snakes captured while surveying habitat edges, 60 were captured in 2536 min searching in open habitats, such as field edges where short grass borders with tall grass or shrubs, and 24 were captured in 2147 min

searching forest edges, where fields or shrubs border with trees. Therefore, in fields we searched approximately 42 min for every snake captured and in forests we searched 89 min for each snake captured. However, there is no significant effect of habitat type on snake capture, after controlling for search time ($F_{1,8} = 0.79$, $P = 0.40$).

For all Northwestern Gartersnakes sampled, six variables were significant at the $P < 0.25$ level (Table 1). We fitted 20 models overall, 12 models had a $\Delta AIC_c < 7$ (Table 2), three of which had $\Delta AIC_c < 2$ (Table 2). Habitat edges where we found Northwestern Gartersnakes have lower proportions of bare ground and woody vegetation than was available at random points (Table 3). Northwestern Gartersnakes are also associated with locations with high proportions of potential cover objects and herbaceous vegetation (Table 3). However, the confidence limit for herbaceous vegetation overlaps zero indicating the relationship is non-significant (Table 3). Northwestern Gartersnakes also used habitat edges with some canopy cover (Table 3), despite that we typically found them in fields rather than forests.

Discussion

Our results suggest that Northwestern Gartersnakes are associated with habitat edges. One potential criticism of this conclusion is that it is biased by the differential visibility of snakes in different habitats. That is,

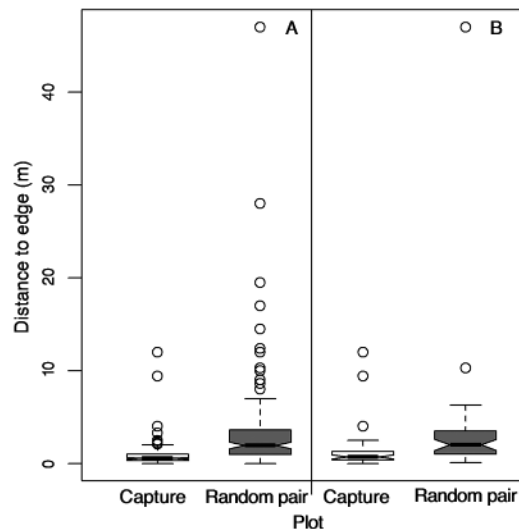


FIGURE 1. Boxplots of Distance to edge (m) at Northwestern Gartersnake (*Thamnophis ordinoides*) capture plots (white) and random-paired plots (grey). A) All captures and paired-random plots, $n = 130$, $W = 760.5$, $P < 0.0001$. B) Captures and paired-random plots with edge searches removed, $n = 46$, $W = 165.5$, $P = 0.003$. Whiskers extend to 1.5 times the interquartile range; beyond the whiskers extreme values are indicated as hollow circles.

TABLE 2. Log-likelihood and associated values for models within 7 AIC_c of the best matched pair logistic regression model for Northwestern Gartersnakes (*Thamnophis ordinoides*) captured while surveying edges. Model 6 is the global model; 20 models were tested overall.

Model	Model ID	Log-likelihood	k	AIC_c	ΔAIC_c	Akaike weight
Canopy + Litter + Cover + BareGround	1	-41.49	4	91.48	0.00	0.34
Canopy + Litter + CoverObj. + WoodyVeg. + BareGround	2	-41.24	5	93.25	1.77	0.14
HerbVeg + Canopy + Litter + CoverObj + BareGround	3	-41.35	5	93.47	1.99	0.13
Canopy + Litter + BareGround	4	-43.81	3	93.91	2.43	0.10
Litter + CoverObj + BareGround	5	-44.10	3	94.51	3.03	0.08
HerbVeg + Canopy + Litter + CoverObj + WoodyVeg + BareGround	6	-41.14	6	95.37	3.89	0.05
HerbVeg + Canopy + Litter + BareGround	7	-43.63	4	95.76	4.28	0.04
Canopy + Litter + WoodyVeg + BareGround	8	-43.76	4	96.02	4.54	0.04
HerbVeg + Litter + CoverObj + BareGround	9	-44.08	4	96.66	5.18	0.03
Litter + WoodyVeg + CoverObj + BareGround	10	-44.10	4	96.72	5.23	0.03
Litter + BareGround	11	-46.57	2	97.29	5.81	0.02
HerbVeg + Canopy + Litter + BareGround + WoodyVeg	12	-43.60	5	97.97	6.48	0.01

TABLE 3. Variables included in averaged matched pair logistic regression model from the top three candidate models ($\Delta AIC_c < 2$) for Northwestern Gartersnakes (*Thamnophis ordinoides*) captured while surveying edges. Table includes estimates, standard error, and 95% confidence intervals (CI).

Variable	Estimate	Std. error	95% CI
Litter	-0.237	0.045	-0.324 -0.148
CoverObj	0.283	0.112	0.062 0.500
BareGround	-0.044	0.011	-0.065 -0.022
Canopy	0.013	0.004	0.006 0.020
WoodyVeg	-0.017	0.003	-0.024 -0.011
HerbVeg	0.003	0.003	-0.002 0.008

rather than snakes favouring edges, edges favour visibility of snakes. That said, radio-telemetry studies of other species have shown that edges are preferred habitats for some species of snakes (Row and Blouin-Demers 2006; Wisler *et al.* 2008; Reading and Jofré 2009), consistent with our findings. Thus, this conclusion is a viable hypothesis for more comprehensive future tests of habitat use in Northwestern Gartersnakes.

Snakes may use edges for multiple reasons (Row and Blouin-Demers 2006; Reading and Jofré 2009), including the possibility that edges provide thermal gradients in close proximity to vegetative cover that can be a source of prey and/or provide an escape refuge from predators. Common Gartersnakes (*Thamnophis sirtalis*) used basking sites beside paths, where they were partially hidden in vegetation but remained exposed to sunlight, and this could reflect a trade off between the need to bask and predator avoidance (Burger *et al.* 2004).

When forests are fragmented, edges are created that are generally warmer than the interior forest (Murcia 1995). It is likely that edges of fields, where we typically found Northwestern Gartersnakes, would maintain thermal gradients in much the same way as would a forest edge. Northwestern Gartersnakes frequently consume slugs (Gregory 1984) and slugs in the genus *Arion* are more abundant at field edges than in fields (Eggenschwiler *et al.* 2013). Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*) in Ontario (Harvey and Weatherhead 2006) and Western Gartersnakes (*Thamnophis elegans*) in New Mexico (Szaro *et al.* 1985) also were regularly found near vegetative cover. We frequently saw potential predators at our 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 actually select locations 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 (*Hoplocephalus bungaroides*) 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, except for gravid females that were generally found in the open (Gregory 2009). Furthermore, the addition of cover objects to survey plots increased the number of snakes detected, including Common Gartersnakes, in field and forest habitats (Halliday and Blouin-Demers 2015). In our 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. Cover objects remained important even when snakes captured underneath them were excluded from analyses. This underscores the importance of cover objects to Northwestern Gartersnakes and supports our survey method because we were able to determine that cover objects are important to this species even while omitting those individuals found under cover and out of view.

The apparent use of sites with low litter depth and low proportions of bare ground and canopy cover 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 clearcuts with no canopy cover and very little litter (Todd and Andrews 2008). One of these species, the Northern Redbelly Snake (*Storeria occipitomaculata*), is found in similar habitats to those used by the Northwestern Gartersnake and also eats slugs and earthworms (Gilhen 1984; Semlitsch and Moran 1984), although, unlike Northwestern Gartersnakes, Northern Redbelly Snakes are active both day and night, rather than just diurnally (P.T.G., unpublished data). Also, grasssnakes in agricultural areas in Switzerland were found at sites with lower proportions of organic litter (Wisler *et al.* 2008). Perhaps shallow litter and canopy cover provide a balance between thermal quality and cover because snakes can bask near the surface while remaining partially obscured within the litter and some shade to avoid extremely high temperatures. Alternatively, because this study relied on visual encounter surveys to find snakes it is also possible that the apparent use of sites with low litter depth is due to the difficulty in detecting snakes in areas of deep litter, rather than an actual increase in abundance where litter is shallow. Further research is required to test these hypotheses.

We also found Northwestern Gartersnakes at locations with higher proportions of woody vegetation 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.

Unlike many other studies of habitat use by snakes (Harvey and Weatherhead 2006; Pattishall and Cundall 2009; Row *et al.* 2012), our study relied on visual encounter surveys, rather than radio-telemetry, and was therefore limited to a description of the habitat occupied by snakes that we could detect. One advantage of this approach is that we base our conclusions on habitat characteristics of locations of many individuals, rather than the small samples of individuals typical of radio-telemetry studies (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 we took. Unfortunately, except for the largest adult females, the small size of the snakes we studied precluded use of radio-telemetry and the approach that we took may be the only one feasible for small snakes that are generally understudied compared to larger species (Blouin-Demers *et al.* 2007). It is almost certain that Northwestern Gartersnakes use some habitat features in which we 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 among 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, over short time periods, to track snakes that are too small for radio-telemetry. Also, we acknowledge that separating our capture and paired points by a random distance between 1 m and 50 m would have been superior to separating them by 50 m every time. However, due to the extreme heterogeneity of the habitat at our field sites the likelihood of a random point being near an edge was very high.

The need to thermoregulate drives habitat use patterns for these animals, and field edges presumably provide temperature gradients that are vital for many aspects of their lives. In urban parks, the maintenance of trail systems and grassy fields for recreation provides edges that snakes will use, provided that vegetated areas are available in which snakes can forage and escape predators. 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 Saanich. Rocks and logs are often removed from areas within parks that are designated for recreation, sports fields or trails, reducing cover avail-

ability 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. Park managers that wish to balance snake habitat and recreation opportunities should maintain parks as a matrix of natural areas, trails, and sports fields that provide thermal gradients, foraging opportunities, and cover.

Ultimately, visual encounter surveys allowed us to obtain preliminary descriptions of patterns of habitat use on edges for Northwestern Gartersnakes. However, due to likely differences in detectability of snakes in different habitats, we do not claim that our study demonstrates preference by Northwestern Gartersnakes for edges relative to other habitats (although that remains a working hypothesis for future test), but it does suggest that these snakes commonly use such habitats and that those habitats are therefore important. Ideally, studies of habitat use for small snake species would incorporate visual encounter surveys, including inspection of cover objects, drift fences, pit-fall traps, and radio-telemetry to address differential use for all size classes.

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Literature Cited

- Bastille-Rousseau, G., D. Fortin, and C. Dussault. 2010. Inference from habitat-selection analysis depends on foraging strategies. *Journal of Animal Ecology* 79: 1157–1163. <https://doi.org/10.1111/j.1365-2656.2010.01737.x>
- Blouin-Demers, G., L. P. G. Bjorgan, and P. J. Weatherhead. 2007. Changes in habitat use and movement patterns with body size in Black Ratsnakes (*Elaphe obsoleta*). *Herpetologica* 63: 421–429. [https://doi.org/10.1655/0018-0831\(2007\)63\[421:CIHUAM\]2.0.CO;2](https://doi.org/10.1655/0018-0831(2007)63[421:CIHUAM]2.0.CO;2)
- Blouin-Demers, G., and P. J. Weatherhead. 2001a. Habitat use by Black Rat Snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82: 2882–2896. <https://doi.org/10.2307/2679968>
- Blouin-Demers, G., and P. J. Weatherhead. 2001b. An experimental test of the link between foraging, habitat selection and thermoregulation in Black Rat Snakes *Elaphe obsoleta obsoleta*. *Journal of Animal Ecology* 70: 1006–1013. <https://doi.org/10.1046/j.0021-8790.2001.00554.x>
- Burger, J., C. Jeitner, H. Jensen, M. Fitzgerald, S. Carlucci, S. Shukla, S. Burke, R. Ramos, and M. Gochfeld. 2004. Habitat use in basking Northern Water (*Nerodia sipedon*)

- and Eastern Garter (*Thamnophis sirtalis*) Snakes in urban New Jersey. *Urban Ecosystems* 7: 17–27. <https://doi.org/10.1023/b:ueco.0000020169.86700.76>
- Burnham, K. P., and D. R. Anderson.** 2002. *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer-Verlag New York Inc., New York, New York, USA. <https://doi.org/10.1007/b97636>
- Calcagno, V.** 2013. *glmulti: model selection and multimodel inference made easy*. R package version 1.0.7. <http://CRAN.R-project.org/package=glmulti>.
- Charland, M. B., and P. T. Gregory.** 1995. Movements and habitat use in gravid and nongravid female garter snakes (Colubridae: *Thamnophis*). *Journal of Zoology* 236: 543–561. <https://doi.org/10.1111/j.1469-7998.1995.tb02731.x>
- DeStefano, S., and R. M. DeGraaf.** 2003. Exploring the ecology of suburban wildlife. *Frontiers in Ecology and the Environment* 1: 95–101. <https://doi.org/10.2307/3868036>
- Dixon-MacCallum, G.** 2013. *Habitat use by Northwestern Gartersnakes (Thamnophis ordinoides) in Saanich, British Columbia*. M.Sc. thesis, University of Victoria, Victoria, British Columbia, Canada.
- Eggenschwiler, L., B. Speiser, A. Bosshard, and K. Jacot.** 2013. Improved field margins highly increase slug activity in Switzerland. *Agronomy for Sustainable Development* 33: 349–354. <https://doi.org/10.1007/s13593-012-0101-1>
- Elzer, A. L., D. A. Pike, J. K. Webb, K. Hammill, R. A. Bradstock, and R. Shine.** 2013. Forest-fire regimes affect thermoregulatory opportunities for terrestrial ectotherms. *Austral Ecology* 38: 190–198. <https://doi.org/10.1111/j.1442-9993.2012.02391.x>
- Fox, J., and S. Weisberg.** 2011. *An R Companion to Applied Regression*. Second edition. Sage Publications, Thousand Oaks, California, USA.
- Furman, B. L. S., B. R. Scheffers, and C. A. Paszkowski.** 2011. The use of fluorescent powdered pigments as a tracking technique for snakes. *Herpetological Conservation and Biology* 6: 473–478.
- Germaine, S. S., and B. F. Wakeling.** 2001. Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. *Biological Conservation* 97: 229–237. [https://doi.org/10.1016/S0006-3207\(00\)00115-4](https://doi.org/10.1016/S0006-3207(00)00115-4)
- Gilhen, J.** 1984. *Amphibians and Reptiles of Nova Scotia*. Nova Scotia Museum, Halifax, Nova Scotia, Canada.
- Gregory, P. T.** 1984. Habitat, diet, and composition of assemblages of garter snakes (*Thamnophis*) at eight sites on Vancouver Island. *Canadian Journal of Zoology* 62: 2013–2022. <https://doi.org/10.1139/z84-295>
- Gregory, P. T.** 2009. Variation in size of cover used by water-snakes (*Nerodia*): do smaller snakes use smaller rocks? *Acta Oecologica* 35: 182–187. <https://doi.org/10.1016/j.actao.2008.09.008>
- Halliday, W. D., and G. Blouin-Demers.** 2015. Efficacy of coverboards for sampling small northern snakes. *Herpetology Notes* 8: 309–314.
- Harvey, D. S., and P. J. Weatherhead.** 2006. A test of the hierarchical model of habitat selection using Eastern Massasauga Rattlesnakes (*Sistrurus c. catenatus*). *Biological Conservation* 130: 206–216. <https://doi.org/10.1016/j.biocon.2005.12.015>
- Helden, A. J., and S. R. Leather.** 2004. Biodiversity on urban roundabouts – Hemiptera, management and the species-area relationship. *Basic and Applied Ecology* 5: 367–377. <https://doi.org/10.1016/j.baec.2004.06.004>
- Hosmer, D. W., and S. Lemeshow.** 2000. *Applied Logistic Regression*. Second edition. John Wiley and Sons Inc., New York, New York, USA. <https://doi.org/10.1002/0471722146>
- Huey, R. B., C. R. Peterson, S. J. Arnold, and W. P. Porter.** 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology* 70: 931–944. <https://doi.org/10.2307/1941360>
- Hurlbert, S. H.** 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211. <https://doi.org/10.2307/1942661>
- Johnson, M. D.** 2007. Measuring habitat quality: a review. *The Condor* 109: 489–504. <https://doi.org/10.1650/8347.1>
- Lawson, P. M. A.** 1991. *Movement patterns and orientation mechanisms in garter snakes*. M.Sc. thesis, University of Victoria, Victoria, British Columbia, Canada.
- Lutterschmidt, W. I., and H. K. Reinert.** 1990. The effect of ingested transmitters upon the temperature preference of the Northern Water Snake, *Nerodia S. sipedon*. *Herpetologica* 46: 39–42.
- Madsen, T.** 1987. Cost of reproduction and female life-history tactics in a population of Grass Snakes, *Natrix natrix*, in southern Sweden. *Oikos* 49: 129–132. <https://doi.org/10.2307/3566017>
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson.** 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Kluwer Academic, Dordrecht, the Netherlands, Boston, Massachusetts, USA. <https://doi.org/10.1007/978-94-011-1558-2>
- Mazerolle, M. J.** 2006. Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia* 27: 169–180. <https://doi.org/10.1163/15685380677239922>
- Molloy, I. A.** 2011. *Habitat distribution of the amphibians and reptiles in the city of Plovdiv, Bulgaria*. *Biharean Biologist* 5: 25–31.
- Murcia, C.** 1995. Edge effects in fragmented forests: Implications for conservation. *Trends in Ecology & Evolution* 10: 58–62. [https://doi.org/10.1016/S0169-5347\(00\)88977-6](https://doi.org/10.1016/S0169-5347(00)88977-6)
- Pattishall, A., and D. Cundall.** 2009. Habitat use by Synurbic Watersnakes (*Nerodia sipedon*). *Herpetologica* 65: 183–198. <https://doi.org/10.1655/08-038r2.1>
- R Core Team.** 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Reading, C. J., and G. M. Jofré.** 2009. Habitat selection and range size of Grass Snakes *Natrix natrix* in an agricultural landscape in southern England. *Amphibia-Reptilia* 30: 379–388. <https://doi.org/10.1163/156853809788795164>
- Reinert, H. K.** 1993. Habitat selection in snakes. Pages 201–240 in *Snakes: Ecology and Behavior*. Edited by R. A. Seigel and J. T. Collins. McGraw-Hill Inc., Whitby, Ontario, Canada.
- Reinert, H. K., and D. Cundall.** 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982: 702–705. <https://doi.org/10.2307/1444674>
- Row, J. R., and G. Blouin-Demers.** 2006. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. *Ecoscience* 13: 443–450. [https://doi.org/10.2980/1195-6860\(2006\)13\[443:tqhsa\]2.0.co;2](https://doi.org/10.2980/1195-6860(2006)13[443:tqhsa]2.0.co;2)
- Row, J. R., G. Blouin-Demers, and S. C. Loughheed.** 2012. Movements and habitat use of Eastern Foxsnakes (*Pantherophis gloydi*) in two areas varying in size and fragmentation. *Journal of Herpetology* 46: 94–99. <https://doi.org/10.1670/10-262>

- Semlitsch, R. D., and G. B. Moran.** 1984. Ecology of the Redbelly Snake (*Storeria occipitomaculata*) using mesic habitats in South Carolina. *American Midland Naturalist* 111: 33–40. <https://doi.org/10.2307/2425539>
- Shew, J. J., B. D. Greene, and F. E. Durbian.** 2012. Spatial ecology and habitat use of the Western Foxsnake (*Pantherophis vulpinus*) on Squaw Creek National Wildlife Refuge (Missouri). *Journal of Herpetology* 46: 539–548. <https://doi.org/10.1670/10-111>
- Soulé, M. E.** 1991. Land use planning and wildlife maintenance: guidelines for conserving wildlife in an urban landscape. *Journal of the American Planning Association* 57: 313–323. <https://doi.org/10.1080/01944369108975502>
- Stebbins, R. C.** 2003. *A Field Guide to Western Reptiles and Amphibians*. Third edition. Houghton Mifflin, Boston, Massachusetts, USA.
- Stevenson, R. D., C. R. Peterson, and J. S. Tsuji.** 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the Wandering Garter Snake. *Physiological Zoology* 58: 46–57. <https://doi.org/10.1086/physzool.58.1.30161219>
- Stewart, G. R.** 1968. Some observations on the natural history of two Oregon garter snakes (Genus *Thamnophis*). *Journal of Herpetology* 2: 71–86. <https://doi.org/10.2307/1563105>
- Steyerberg, E. W., F. E. Harrell, Jr., G. J. J. Borsboom, M. J. Eijkemans, Y. Vergouwe, and J. D. F. Habbema.** 2001. Internal validation of predictive models: efficiency of some procedures for logistic regression analysis. *Journal of Clinical Epidemiology* 54: 774–781. [https://doi.org/10.1016/S0895-4356\(01\)00341-9](https://doi.org/10.1016/S0895-4356(01)00341-9)
- Szaro, R. C., S. C. Belfit, J. K. Aitkin, and J. N. Rinne.** 1985. Impact of grazing on a riparian garter snake. Pages 359–363 *in* *Riparian Ecosystems and their Management: Reconciling Conflicting Uses*. USDA Forest Service General Technical Report RM-120. Edited by R. R. Johnson, C. D. Ziedell, D. R. Patton, P. F. Folliott, and F. H. Hamre. U.S. Department of Agriculture Forest Service, Fort Collins, Colorado, USA.
- Thomas, D. L., and E. J. Taylor.** 2006. Study designs and tests for comparing resource use and availability II. *The Journal of Wildlife Management* 70: 324–336. [https://doi.org/10.2193/0022-541x\(2006\)70\[324:sdatfc\]2.0.co;2](https://doi.org/10.2193/0022-541x(2006)70[324:sdatfc]2.0.co;2)
- Todd, B. D., and K. M. Andrews.** 2008. Response of a reptile guild to forest harvesting. *Conservation Biology* 22: 753–761. <https://doi.org/10.1111/j.1523-1739.2008.00916.x>
- Weatherhead, P. J., J. H. Sperry, G. L. F. Carfagno, and G. Blouin-Demers.** 2012. Latitudinal variation in thermal ecology of North American ratsnakes and its implications for the effect of climate warming on snakes. *Journal of Thermal Biology* 37: 273–281. <https://doi.org/10.1016/j.jtherbio.2011.03.008>
- Webb, J. K., and R. Shine.** 1998. Using thermal ecology to predict retreat-site selection by an endangered snake species. *Biological Conservation* 86: 233–242. [https://doi.org/10.1016/S0006-3207\(97\)00180-8](https://doi.org/10.1016/S0006-3207(97)00180-8)
- Webb, J. K., and M. J. Whiting.** 2005. Why don't small snakes bask? Juvenile Broad-Headed Snakes trade thermal benefits for safety. *Oikos* 110: 515–522. <https://doi.org/10.1111/j.0030-1299.2005.13722.x>
- Westfall, P. H., and S. S. Young.** 1993. *Resampling-Based Multiple Testing: Examples and Methods for P-Value Adjustment*. John Wiley and Sons Inc., New York, New York, USA.
- Wisler, C., U. Hofer, and R. Arlettaz.** 2008. Snakes and monocultures: habitat selection and movements of female Grass Snakes (*Natrix natrix* L.) in an agricultural landscape. *Journal of Herpetology* 42: 337–346. <https://doi.org/10.1670/07-027.1>

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