Do roads affect the abundance of garter (*Thamnophis sirtalis*) and redbelly snakes (*Storeria occipitomaculata*)?

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ABSTRACT

The greatest driver of the current global biodiversity crisis is habitat loss. Roads are a major contributor to habitat loss because they destroy and fragment habitat, in addition to causing direct mortality. Animals may respond to roads either by avoiding them, thus leading to population isolation, or by attempting to cross them, thus potentially leading to increased mortality and, if so, also to population isolation. I studied the impact of road density on abundance of two northern snake species: the redbelly snake (*Storeria occipitomaculata*) and the garter snake (*Thamnophis sirtalis*). I hypothesized that roads are detrimental to snake populations due to road avoidance and road mortality. Therefore, I predicted that snakes should be less abundant in sites with higher road density in their surroundings. I deployed cover boards at 28 old field sites along a gradient of road density in 2020 and in 2021. I visited sites weekly and counted the number of individuals of both species. I captured fewer garter snakes at sites surrounded by more roads, and fewer redbelly snakes at sites enclosed by more roads. The effect of roads on number of snakes is modest, but could be indicative of decreasing population size, which could in turn lead to loss of ecological function.

RÉSUMÉ

Le plus grand moteur de la crise mondiale actuelle de la biodiversité est la perte d'habitat. Les routes contribuent grandement à la perte d'habitat parce qu'elles détruisent et fragmentent l'habitat, en plus de causer de la mortalité directe. Les animaux peuvent réagir aux routes soit en les évitant, entraînant ainsi l'isolement des populations, soit en tentant de les traverser, entraînant ainsi potentiellement une mortalité accrue et également l'isolement des populations. J'ai étudié l'impact de la densité des routes sur l'abondance de deux espèces de couleuvres nordiques : la couleuvre à ventre rouge (*Storeria occipitomaculata)* et la couleuvre rayée (*Thamnophis sirtalis*). J'ai émis l'hypothèse que les routes sont néfastes pour les populations de serpents en raison de l'évitement des routes et de la mortalité routière. Par conséquent, j'ai prédit que les couleuvres devraient être moins abondantes dans les sites avec une densité routière plus élevée dans leurs environs. J'ai déployé des plaques abris sur 28 sites de champs en friche le long d'un gradient de densité de routes en 2020 et en 2021. J'ai visité les sites chaque semaine et compté le nombre d'individus des deux espèces. J'ai capturé moins de couleuvres rayées et moins de couleuvres à ventre rouge aux sites entourés de plus de routes. L'effet des routes sur le nombre de couleuvres est modeste, mais pourrait indiquer une diminution de la taille de la population, ce qui pourrait à son tour entraîner une perte de fonction écologique.

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INTRODUCTION

Since 1900, the rate of extinction for vertebrates has increased by approximately three orders of magnitude from the estimated background extinction rate (Alroy 2015; Pimm et al. 2015). Almost 500 vertebrate extinctions have been recorded in the last century and the IUCN reports that almost one third of species assessed are threatened with extinction (IUCN 2019). Because many species have yet to be assessed by the IUCN, and because many species experiencing declines are listed as “no concern” (Ceballos et al. 2017), the IUCN reports are an underestimate of the proportion of species currently faced with extinction. Additionally, population declines may be sufficient to cause loss of ecological interactions, such as predator-prey relationships, resulting in catastrophic ecosystem changes without those species necessarily becoming extinct (Hull et al. 2015; Valiente-Banuet et al. 2015), a phenomenon known as ecological extinction (Valiente-Banuet et al. 2015). Ecosystem shifts following population declines and loss of ecological interactions can make it difficult or impossible to recover previous species and ecological functions (Jackson 2008).

The greatest driver of global biodiversity loss is anthropogenic land use (Pimm and Raven 2000; Sala et al. 2000; Thomas et al. 2004; Didham et al. 2005; Valiente-Banuet et al. 2015). Globally, land use outranked other concerns such as climate change and ocean acidification as the greatest threat to biodiversity, and potentially a source of major changes in ecological composition in the future (Sala et al. 2000; Newbold et al. 2020).

Anthropogenic land use takes many forms. It includes outright habitat loss, whereby suitable habitat is rendered completely unsuitable for resident species (Fahrig 1997, 2003; Paterson et al. 2021); habitat degradation, whereby suitable habitat is rendered less suitable for resident species (Heinrichs et al. 2016); and habitat fragmentation, whereby the ability of animals to move through the habitat is impeded (Fahrig 2003). Habitat loss, degradation, and fragmentation are often concurrent effects of development and other human activities (Fahrig 1997, 2003; Heinrichs et al. 2016).

One of the major contributing factors to habitat loss, degradation, and fragmentation is the construction of roads (Forman et al. 2003; Eigenbrod et al. 2008). Roads render habitat unsuitable for use by animals in several ways, either concurrently or separately. Habitat area may be reduced following the construction of the road and associated features (e.g., ditches, paved shoulders) (Reed et al. 1996; Forman et al. 2003). Remaining habitat may be less suitable for animals due to edge effects (Delgado et al. 2007; Goosem 2007), exposure to noise and chemical pollution, and introduction of invasive species facilitated by transportation (Forman et al. 2003). Degradation of habitat can result in population declines without extirpation. Degraded habitats can have better conservation value than destroyed habitats because populations may be able to recover with habitat restauration (Goldingay and Newell 2017). Animals may respond to roads in one of two ways: they may avoid the road and thus increase population isolation (Frair et al. 2008; Eigenbrod et al. 2009; Delaney et al. 2010; Jackson and Fahrig 2011; Rytwinski and Fahrig 2015); or they may attempt to cross the road and thus increase both mortality and population isolation (Bouchard et al. 2009; Rytwinski and Fahrig 2015). Both behaviours result in population declines in areas of high road density.

Reptiles are more sensitive to habitat disturbance than mammals and birds (Keinath et al. 2017). In a fragmented landscape, reptiles have the lowest presence across habitat patches and the highest sensitivity to patch size relative to other vertebrate taxa (Keinath et al. 2017). Habitat modification results in lower reptile abundance irrespective of phylogeny or climate, making it the strongest predictor of species- and population-level extinction for reptiles (Doherty et al. 2020). Many reptile species, including snakes, are sensitive to habitat disturbance because they have low dispersal capabilities relative to mammals and birds, making it more challenging for them to escape disturbed habitats and relocate to more suitable areas (Reading et al. 2010). In addition, reptiles use behavioural thermoregulation, and the thermal quality of the habitat is altered by roads (Delgado et al. 2007). For example, removal of vegetation along roadsides increases temperatures at ground level (Saunders et al. 1991). In addition, the road surface itself may alter thermal quality of the habitat and reptiles may be attracted to warm road surfaces for thermoregulation (Rudolph et al. 1998; Enge and Wood 2002; Mccardle and Fontenot 2016), which increases their likelihood of being struck by a vehicle. Reptiles are more susceptible to high road mortality relative to mammals and birds (Ashley and Robinson 1996; Choquette and Valliant 2016), because they are slow moving which increases their exposure time on the road surface and likelihood of being struck by a vehicle (Rudolph et al. 1998; Rytwinski and Fahrig 2015). There is also evidence suggesting that snakes and turtles are intentionally targeted by motorists (Ashley et al. 2007). Moreover, roads may be detrimental to reptile populations due to avoidance. Avoidance of roads by snakes has been demonstrated by lower numbers of road crossings than expected by chance (Robson and Blouin-Demers 2013; Paterson et al. 2019) and inferred by decreasing population density in fields with increasing proximity to a road (Patrick and Gibbs 2009).

Garter snakes (*Thamnophis sirtalis*) and redbelly snakes (*Storeria occipitomaculata*) are locally abundant in eastern North America (Retamal Diaz and Blouin-Demers 2017; Halliday and Blouin-Demers 2018), making them ideal species to document variation in snake population abundance in response to changes in road density. To date, to the best of my knowledge, no studies have compared the effect of road density on the abundance of these two species while controlling for habitat type. Garter snakes are generalist predators, feeding on a variety of prey including invertebrates, amphibians, fish, small mammals, and occasionally bird eggs (DeGregorio et al. 2014). Redbelly snakes are specialist predators of soft-bodied invertebrates such as gastropods (Sousa do Amaral 1999; Pisani and Busby 2011). Snakes are commonly by birds and mammals (Sparkman et al. 2013; Tye et al. 2017).

The objective of my research is to determine whether there is a relationship between abundance of garter and redbelly snakes in old fields (their preferred habitat (Carpenter 1952; Halliday and Blouin-Demers 2015, 2016; Retamal Diaz and Blouin-Demers 2017)) and road density in the surrounding area. I hypothesized that roads cause direct mortality and thus population isolation of these two northern snake species. Therefore, I predicted that that I would capture fewer snakes at sites surrounded by more roads than at sites surrounded by fewer roads. I also hypothesized that high road mortality causes snakes to be killed before reaching full size. Thus, I predicted that snakes captured at sites surrounded by more roads would be smaller than those captured at sites surrounded by few roads.

METHODS

Study Sites and Species

Redbelly snakes (*Storeria occipitomaculata*) are small (<30 cm), while garter snakes (*Thamnophis sirtalis*) are larger (typically ~50 cm) snakes that are locally abundant in the Ottawa/Gatineau (Canada) area. Both species are commonly found in old field habitats (Carpenter 1952; Halliday and Blouin-Demers 2015, 2016; Retamal Diaz and Blouin-Demers 2017).

I selected 28 sites in Gatineau Park, the Ottawa Greenbelt, and Stonebridge Golf Club to obtain a gradient of road density (Figure 1). Of these 28 sites, I visited 3 in 2020 only, 9 in 2021 only, and 16 in both years (Figure 1). All sites were old fields (field habitats not currently in use for agriculture), the preferred habitat for small snakes in our area (Carpenter 1952; Halliday and Blouin-Demers 2015, 2016; Retamal Diaz and Blouin-Demers 2017). The plant communities at all sites were dominated by grasses (mainly *Poa* and *Phleum spp*) and forbs (mainly *Solidago* and *Trifolium*).

Field Surveys

At each site, I installed 10 to 30 plywood boards (60 x 60 x 1.27 cm) in 200-600 m transects with boards spaced 20 m apart to increase sampling efficacy of snakes (Carpenter 1952; Kjoss and Litvaitis 2001; Halliday and Blouin-Demers 2015). I visited each site approximately once per week between 23 June and 18 October in 2020 for a total of 17 weeks, and between 18 May and 1 October in 2021 for a total of 19 weeks (see Table 1). I visited sites under favourable weather conditions (i.e., clear skies and air temperature between 10 and 30° C).

During each visit, between one and three people walked the length of the transect at a distance of 2 m from one another at a constant pace (Carpenter 1952; Halliday and Blouin-Demers 2015). We overturned each board and any snakes found under the board were captured. Snakes encountered between boards while walking the transect were also captured, but this represented very few snakes (see Results).

Captured snakes were identified to species and the few individuals from non-target species were released. Non-target species encountered included milk snakes (*Lampropeltis triangulum*), ringneck snakes (*Diadophis punctatus*), northern water snakes (*Nerodia sipedon*), and smooth green snakes (*Opheodrys vernalis*) (see Results). Target species were measured from the tip of the snout to the cloacal opening (snout-vent length: SVL). Larger snakes were sexed by inserting a lubricated probe into the cloaca towards the tail. Insertion depths of 1-2 mm were recorded as female and insertion depths > 2 mm were recorded as male. Smaller snakes too small to probe were recorded as juveniles (Patrick and Gibbs 2009). The date, time, and location of each capture were recorded using a handheld GPS device (Garmin GPSMap 78s). Air temperature and weather conditions were obtained from the Government of Canada records taken at the Ottawa International Airport (https://climate.weather.gc.ca/historical_data/search_historic_data_e.html) situated 8.6 to 44.1 km from my study sites.

Snakes that had not previously been captured were uniquely marked by branding on the ventral scales anterior to the cloaca with a disposable medical cautery unit (Bovie Change-A-Tip Low Temperature Cautery Kit) following Winne et al. (2006). Mark combinations were unique to individuals within province. Snakes that had previously been captured and were already marked were measured and sexed to confirm the identity of the animal, and their individual ID number was recorded. I standardized the number of unique individual snakes caught at each site by dividing by the number of visits per site, and multiplying by the proportion of boards given that 20 boards was the standard (thus number of snakes from a site with 20 boards was multiplied by 1, number of snakes from a site with 10 boards was multiplied by 0.5, etc). The standardized number of unique individual snakes was used in all further analyses except where stated otherwise.

Habitat Variables

Seven habitat variables were considered for modelling. These were road density, percent cover of field, forest, urban, and water, whether a site was mowed annually, and the number of sides of a site in contact with a road (Table 2).

I derived percent cover of the four habitat types from the Ontario Land Cover Compilation Version 2.0 (OLCC) (https://geohub.lio.gov.on.ca/documents/7aa998fdf100434da27a41f1c637382c/about) and the Comptes des Terres du Québec (CTQ) (https://www.donneesquebec.ca/recherche/fr/dataset/comptes-des-terres-du-quebec-meridional-changement-de-la-couverture-terrestre). I combined the 29 land cover categories for OLCC and 11 land cover categories for CTQ into the four categories outlined above (Tables 3, 4), and merged the two land cover datasets using ArcGIS Pro Version 2.7.3 (Esri 2020) . The old fields used as study sites were recorded as agricultural fields in the CTQ dataset, and agriculture or undifferentiated rural land in the OLCC dataset, so both these land classes were categorized as "fields". Road density was derived from the 2020 Canada Road Network downloaded from Statistics Canada (https://www12.statcan.gc.ca/census-recensement/2011/geo/RNF-FRR/index-eng.cfm).

I constructed buffers around each site in 100 m increments from 100-1000 m using ArcGIS Pro. Both redbelly and garter snakes have been reported travelling around 500 m in a 24 hour period (Blanchard 1937; Carpenter 1952), but I was unable to find recent data on home range area for either snake species. I chose 1000 m as the maximum buffer distance to ensure that I included the appropriate area which individuals of either species are likely to experience in a season (Jackson and Fahrig 2015). This distance is also frequently used in landscape studies of small vertebrates (Jackson and Fahrig 2015; Moraga et al. 2019). Because most snakes were captured under cover boards (see Results), the cover board transects were used to centre the buffers. The area of each buffer (km^2) and total length of roads within buffers (km) were used to determine road density for each buffer increment. The percent covers of each of the four land classes within each buffer were calculated with the Tabulate Area tool for ArcGIS Pro (https://hub.arcgis.com/content/3528bd72847c439f88190a137a1d0e67/about). I determined the number of sides (maximum = 4) in contact with a road visually in ArcGIS Pro using data from the Canada Road Network. A site was deemed in contact with a road if there was a road within a buffer. Whether a field was mowed was reported by Gatineau Park and Stonebridge Golf Club staff.

Continuous predictor variables (Table 2) were scaled using the scale function in R. Mean SVL for both species did not deviate from normality either visually or using the Shapiro-Wilk test (Garter: W = 0.94, p = 0.26; Redbelly: W = 0.94, p = 0.21), and was not transformed. For mean SVL, sites where no snakes were captured were omitted from analysis. This resulted in N = 21 sites for garter snakes, and N = 20 for redbelly snakes.

To determine the scale of maximum effect, I calculated Pearson's correlation coefficient between the standardized number of snakes (see 'Field Surveys'), and the habitat variables (ROADS, %FIELD, %FOREST, %URBAN, %WATER, and SIDES). The buffer distance with the largest absolute correlation for each variable was retained for inclusion in the final model (Jackson and Fahrig 2015; Čapkun-Huot et al. 2021; Fyson and Blouin-Demers 2021). I repeated this for mean SVL for both species at each site.

Modeling

The buffer distance with the largest absolute correlation for each continuous variable, whether the site was mowed, and the number of sides in contact with a road were included in the full model for each of the dependent variables. I also included Julian date, temperature, and time of day as continuous variables, and number of boards at each site (10, 20, or 30) as a categorical variable in the full models. I included site as a random effect.

I tested each full model for variance inflation using the gvif() function in the package "car" (Fox and Weisberg 2019). I removed any explanatory variables with gvif scores ≥2 from the final models. I removed the variables "forest" and "sides" from the model for garter snake count, "forest" from the model for redbelly snake count, "forest", "road" and "sides" from the model for garter snake SVL, and "urban" from the model for redbelly snake SVL due to multicollinearity.

I performed a correlation analysis for continuous predictor variables in all of the full models using the cor() function in base R. I found high (≥0.7) Pearson's correlation between "urban" and "roads" at the scales used for all models.

Because "urban" and "roads" were highly correlated at the scales used for modeling garter snake and redbelly snake counts, but were not removed from those models due to high multicollinearity, I built candidate models with only one of those variables. I compared the fit of those models using the AIC output from the glmer() function in the "lme4" package in R.

RESULTS

Snake Surveys

In total, I captured 691 individual redbelly snakes 801 times and 354 individual garter snakes 386 times (Tables 5, 6), with 83% of garter snakes and 99% of redbelly snakes captured under cover boards. A higher proportion of redbelly snakes were captured under boards, probably because redbelly snakes are smaller and less visible in the grass than garter snakes. Additionally, 28 milk snakes (*Lampropeltis triangulum*), 5 ring-necked snakes (*Diadophis punctatus*), 3 smooth green snakes (*Opheodrys vernalis*), and 2 common watersnakes (*Nerodia spideon*) were observed during surveys.

Most redbelly snakes were captured once (604, 87%), 66 individuals were captured twice (10%), 16 individuals (3%) were captured three times, 3 individuals were captured 4 times (0.4%), and one individual was captured five times (0.1%). Nine individuals were captured in both 2020 and 2021, 319 individuals were only captured in 2020, and 363 individuals were only captured in 2021.

Most garter snakes were captured once (324 individuals, 93%), 27 individuals (6%) were captured twice, and 3 individuals (0.3%) was captured three times. Four individuals were captured in both 2020 and 2021, 146 individuals were captured only in 2020, and 204 individuals were captured only in 2021. The low number of recaptures for both species of snake suggests that the population sizes are very large.

Predictors for Number of Snakes

The scale of maximum effect varied from 200-1000 m for number of garter snakes, 200-900 m for number of redbelly snakes, 200-800 m for mean SVL of garter snakes, and 200-1000 m for mean SVL of redbelly snakes (Figures 2-5). The habitat variable that best predicted number of garter snakes was road density (Table 7). Time of year, time of day, and number of boards at each site also had moderate, statistically significant effects on the number of garter snakes captured (Table 7). I found more garter snakes at sites surrounded by fewer roads, more snakes earlier in the year, later in the day, and at sites with more boards (i.e., larger sites). The habitat variable that best predicted the number of redbelly snakes was urban area (Table 7). Time of year, time of day, number of boards at each site, and temperature also had moderate, statistically significant effects on the number of redbelly snakes captured (Table 7). I found more redbelly snakes at sites surrounded by less urban habitat, and more snakes earlier in the year, later in the day, at sites with more boards (i.e., larger sites), and when the temperature was cooler. No habitat variables were statistically significant in predicting SVL of either species. Temperature had a moderate effect on the SVL for both species. I found larger snakes of both species when the temperature was warmer. Number of boards had a moderate effect on the SVL of garter snakes. I found larger garter snakes at sites with fewer boards (i.e., smaller sites).

DISCUSSION

What is the relationship between road density and snake abundance?

There may be fewer garter and redbelly snakes where there are more roads because many snakes are being killed on roads. Snakes comprise a large portion of roadkill surveys (Ashley and Robinson 1996; Choquette and Valliant 2016), and increasing road density in an area may force snakes onto roads, especially during dispersal. If populations are reduced by numerous individuals being killed during dispersal (i.e., neonates), I would expect the mean SVL to be larger where there are more roads, due to fewer neonates being captured during the season. While I did find that redbelly snakes were larger at more enclosed sites, and garter snakes were larger at more urbanized sites, neither of these effects were statistically significant (Table 7).

Higher road density may indirectly impact garter and redbelly snake occupancy by decreasing the habitat quality. However, Paterson et al. (2021) found no statistically significant effect of habitat loss, road density, or the interaction between the two, on the occupancy of either garter or redbelly snakes, suggesting that these species might be somewhat resilient to anthropogenic change. Their study was undertaken in a large area (throughout Ontario), and considered road type (paved vs. unpaved, average traffic speed), and anthropogenic land cover, while my study was undertaken in a smaller area (Gatineau and Ottawa), grouped roads together irrespective of type, and considered both anthropogenic and natural land cover types. As well, their study considered occupancy rather than abundance. It is possible that garter and redbelly snakes are sensitive to anthropogenic disturbance when all road and habitat types are considered.

I did not include road type in my models of snake abundance or SVL because of potential issues with statistical power from including numerous predictor variables. Whether or not a road is paved affects the likelihood of crossing by hognose snakes, which avoid crossing paved but not unpaved roads (Robson and Blouin-Demers 2013). Paved road surfaces are hotter than unpaved roads, which could deter snakes from crossing them. Traffic volume and speed are generally higher on paved than unpaved roads, which could also deter snakes due to avoidance of vibrations from vehicles passing. Higher traffic volumes and speeds could also increase the likelihood of road mortality. As well, paved roads are more prevalent in urban areas, while unpaved roads are more prevalent in rural areas, therefore there may be larger populations of snakes in areas with more unpaved roads, causing there to be more road crossings by snakes.

Because abundance is a coarse population measure, roads may have effects on snake populations that I was unable to detect. For example, male and female snakes might experience different degrees of road mortality due to differences in dispersal between the sexes. Sex ratios and dispersal are both male-biased in garter snakes (Shine et al. 2006). Increased road mortality during dispersal could impact sex ratios, which would have negative impacts on populations.

What other factors may impact snake abundance?

In addition to affecting snake abundance, landscape features may also impact road density and placement. Road placement seeks to facilitate human movement while minimizing construction costs. Road density is higher in areas closer to human habitation, and lower in areas where roads are expensive to construct. For example, I found a moderate effect of percent area of water on garter snake abundance. I did not find a strong correlation between percent area of water and road density, however, few roads are built through open water (e.g., lakes, rivers) or wetland (e.g., marshes, bogs) habitat relative to terrestrial habitat.

I captured more redbelly snakes when the temperature was cooler. This may be because cover boards may be warmer and more attractive to snakes when the air temperature is cooler. Further studies could compare the air temperature to temperature under cover boards. There was not a statistically significant effect of temperature on the number of garter snakes captured, but there was a trend for garter snakes captured on cooler days to be smaller. This suggests that smaller garter snakes may be more likely to seek refuge under warm boards when the air temperature is cooler.

What does this mean more broadly for snake populations?

Efforts are currently being made to reduce road mortality for snakes. Typically, these interventions focus on mitigating direct road mortality by installing exclusion fencing (Colley et al. 2017; Boyle et al. 2021), often in tandem with structures such as tunnels which allow animals to move through the environment without crossing the road surface (Colley et al. 2017; Boyle et al. 2021). Response by snakes to both types of intervention is mixed. Exclusion fencing can prevent road access and mortality in massassaugas (Colley et al. 2017), while grey rat snakes are able to climb over certain types of fence (Macpherson et al. 2021), and garter snakes are not always prevented from accessing roads by fencing at all (Boyle et al. 2021). The efficacy of tunnels or other taxon-specific ecopassages is also debated, as snakes sometimes ignore tunnels as often as they use them (Boyle et al. 2021), or begin but do not finish crossing (Colley et al. 2017). Overall, this suggests that even if direct mitigation structures are used, they may not be effective at preventing snake mortality if they are not designed and tested to fit a specific species. Interventions rarely, if ever, focus on mitigating other, sub-lethal effects of roads, such as road avoidance, and reduction in habitat quality surrounding roads.

The substantial effect of water, and open field habitat on garter and redbelly snakes respectively suggests that preservation of those habitat types could be as important for conservation of these species as mitigating road mortality. Habitat specialists, particularly grassland species, are more sensitive to habitat fragmentation than habitat generalists, and species which do not live in grasslands (Keinath et al. 2017). As well, degraded habitat can be restaured as part of species recovery, as long as endemic species are still present in the habitat (Goldingay and Newell 2017). This may be a way to improve conservation outcomes for species impacted by roads when mitigation of direct mortality is less effective.

Future studies with greater numbers of sites should consider testing the interaction between habitat type and road density on abundance of garter and redbelly snakes.

Study Limitations and Future Directions

This study was primarily limited by the small number of sites, which restricted the number of predictive variables that could be used in modelling. Future studies with more sites could include more habitat variables such as road type and traffic density, and more demographic variables such as sex, reproductive status, and age class of snakes.

Abundance as a measure of population size likely impacted the accuracy of the results. Recapture rate was too low to use mark-recapture models to estimate population size more accurately. Recapture rate could be improved by visiting sites more often (e.g., two or three times per week).

Because this study was conducted over only two years, I was unable to detect long-term changes in snake populations. Animal populations may change in response to changes in road density, urbanization, and traffic, and these population changes may take longer than the duration of this study. Long term (i.e., at least 5-10 years) studies could also estimate growth rate and fecundity of snakes in response to increasing road density and urbanization.

Finally, future studies could attempt to determine the relative contributions of road mortality and avoidance on snake populations. Mark-recapture models of population size can estimate mortality. Roadkill surveys could be used in tandem with population models to estimate proportions of snake populations being killed on roads. Genetic tests of nearby populations could determine whether individuals are successfully dispersing between populations separated by roads, and the degree of genetic diversity provided by dispersal.

CONCLUSION

I found that roads do have a modest, negative impact on number of garter and redbelly snakes in old fields. The negative impact of roads could be due either to direct mortality, or to habitat degradation, or both. Future studies could investigate the relative contributions of mortality and avoidance. Though both species are locally abundant, and neither is considered "at risk", species-level declines are caused, and preceded, by population-level declines. Declining populations can also result in a loss of ecological interactions and ecological extinction, despite that species persisting at low numbers (Hull et al. 2015; Valiente-Banuet et al. 2015).

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TABLES

Table 1. Field sites surveyed for garter and redbelly snakes Ottawa (ON) and Gatineau (QC), Canada. Sites were visited between 23 June – 18 October 2020, and 18 May – 1 October 2021. The total number of visits over both years is presented. Between 10 and 30 plywood coverboards were installed in a transect at each site to increase sampling efficacy of snakes.

Site (Abbreviation)	Coordinates	Total Visits	Boards Installed
Bruce Pit (BP)	45.32, -75.80	20	20
Chemin du Lac Philippe (PH)	45.63, -76.01	28	20
Chemin Pilon 1 (PLA)	45.55, -76.05	40	10
Chemin Pilon 2 (PLB)	45.55, -76.04	31	20
Corkstown Rd. & Moodie Dr. (CT)	45.34, -75.84	17	20
Dolman Ridge Road (MB)	45.40, -75.53	41	20
Dundonald Dr. (DD)	45.24, -75.72	17	20
Gatineau Park P15 (P15)	45.58, -75.90	29	20
Gatineau Park P16 1 (P16)	45.57, -75.89	38	20
Gatineau Park P16 2 (P16B)	45.57, -75.88	15	20
Gatineau Park P17 (P17)	45.62, -75.93	28	20
Gatineau Park P8 (P8)	45.50, -75.82	33	20
Gatineau Park Trail 26 (GB)	45.45, -75.77	19	20
Gatineau Parkway (GP)	45.46, -75.78	31	20
Golflinks Dr. 1 (GL1)	45.25, -75.72	17	10
Golflinks Dr. 2 (GL2)	45.25, -75.72	17	20
Greenbelt P3 (P3)	45.33, -75.86	21	20
Greenbelt P5 (P5)	45.30, -75.87	38	20
Greenbelt Trail 24 (RR)	45.30, -75.85	40	20
Greenbelt Trail 25 (CC)	45.28, -75.83	37	20
Greenbelt Trail 29 (SK)	45.31, -75.79	20	20
Greenbelt Trail 51 (N51)	45.40, -75.58	36	30

Kilmarnock Way (KM)	45.24, -75.72	17	20
Luskville Falls (LV)	45,53, -75.99	37	20
Riverstone Dr. (SB2)	45.26, -75.72	14	20
Stromness Pvt. (SB)	45.24, -75.71	36	20
Watts Creek Pathway (WC)	45.34, -75.88	40	20
Watts Creek Pathway Parking (WP)	45.32, -75.88	18	20

Table 2. Variables considered for inclusion in models of number and SVL of garter and redbelly snakes in Ottawa (ON) and Gatineau (QC), Canada. Variables were either continuous, or categorical. Continuous variables included road density in km/km^2, percent cover of four different habitat types (field, forest, urban, and water), Julian date, temperature, and time of day. Categorical variables included whether a site is mowed annually, the number of sides of a site in contact with a road, and the number of boards at each site. Site was included as a random effect. Road density was derived from data obtained by Statistics Canada. Percent land cover for each of the four habitat types was derived from the Ontario Land Cover Compilation (OLCC) and Comptes de Terres du Quebec (CTQ). Number of sides in contact with a road was determined visually. Whether a site was mowed was reported by Gatineau Park or Stonebridge Golf Club. Temperature data were obtained from Statistics Canada.

Variable	Type	Description
road	Continuous	Road density (Km road / km^2 area)
field	Continuous	Field (% cover)
forest	Continuous	Forest (% cover)
urban	Continuous	Urban (% cover)
water	Continuous	Water (% cover)
mowed	Categorical (binomial)	Site mowed annually or site not mowed (0, 1)
sides	Categorical	# sides in contact with a road within each buffer (0-4)
date	Continuous	Julian date
temperature	Continuous	Air temperature in degrees C
time	Continuous	Time of day
boards	Categorical	Number of boards installed at each site (10, 20, 30)
site		Random effect

Table 3. Classification of land cover types in Ottawa, Ontario, Canada. Original classification is derived from the OLCC dataset. Of the original 29 land cover types, 23 were reclassified into one of four habitat types used in my analysis (field, forest, urban, and water). The remaining 6 were classified "n/a", as they do not fit into one of the four types, were found in very low quantities in the study area, and were not likely to impact snake distribution.

Original Classification	Reclassification
Clear Open Water	Water
Turbid Water	Water
Shoreline	Water
Mudflats	Water
Marsh	Water
Swamp	Water
Fen	Water
Bog	Water
Heath	Field
Sparse Treed	Forest
Treed Upland	Forest
Deciduous Treed	Forest
Mixed Treed	Forest
Coniferous Treed	Forest
Plantations – Trees Cultivated	Urban
Hedge Rows	Urban
Disturbance	Urban
Open Cliff and Talus	n/a
Alvar	n/a
Sand Barren and Dune	n/a
Open Tallgrass Prairie	Field
Tallgrass Savannah	Field
Tallgrass Woodland	Field
Sand / Gravel / Mine Tailings / Extraction	Urban

Bedrock	n/a
Community / Infrastructure	Urban
Agriculture and Undifferentiated Rural Land Use	Field
Other	n/a
Cloud / Shadow	n/a

Table 4. Classification of land cover types in Gatineau, Quebec, Canada. Original classification is derived from the CTQ dataset. Of the original 11 land cover types, 9 were reclassified into one of four habitat types used in my analysis (field, forest, urban, and water). The remaining 2 were classified "n/a", as they do not fit into one of the four types, were found in very low quantities in the study area, and were not likely to impact snake distribution.

Original Classification	Reclassification
Surfaces artificielles	Urban
Terres agricoles	Field
Milieux humides forestiers	Water
Milieux humides herbacés ou arbustifs	Water
Plans et course d'eau intérieure	Water
Forêts de conifers à couvert fermé	Forest
Forêts de feuilles à couvert fermé	Forest
Forêts mixtes à couvert fermé	Forest
Forêts à couvert ouvert	Forest
Pas de données	n/a
En attente de traitement	n/a

Table 5. Number of unique individual garter snakes marked in Ottawa (ON) and Gatineau (QC), Canada. Snakes marked in 2020 were captured between 23 June and 18 October, and snakes marked in 2021 were captured between 18 May and 1 October. Number of adult female (#F), adult male (#M), and juvenile or snakes for which sex could not be determined (#J / U) are presented for each site in each year. Totals per site, per year, and per age/sex category are also presented. Blank cells indicate sites that were not visited in that year.

	2020				2021				Both Years
Site	# F	# M	# J / U	**Total**	# F	# M	# J/U	**Total**	**Total**
BP	4	3	12	**19**					**19**
CC	1	0	0	**1**	0	1	3	**4**	**5**
CT					1	2	2	**5**	**5**
DD					0	0	0	**0**	**0**
GB					2	2	0	**4**	**4**
GLA					0	0	0	**0**	**0**
GLB					1	0	0	**1**	**1**
GP	1	0	1	**2**	2	1	7	**10**	**12**
KM					0	0	0	**0**	**0**
LV	1	1	9	**11**	4	2	20	**26**	**37**
MB	10	7	31	**48**	6	1	13	**20**	**68**
N51	0	1	1	**2**	1	1	1	**3**	**5**
P15	0	0	0	**0**	0	0	0	**0**	**0**
P16	0	0	1	**1**	3	1	22	**26**	**27**
P16B	0	0	0	**0**	0	0	0	**0**	**0**
P17	0	0	0	**0**	0	0	0	**0**	**0**
P3					2	0	1	**3**	**3**
P5	1	0	2	**3**	5	0	10	**15**	**18**
P8	0	0	0	**0**	1	1	4	**6**	**6**
PH	0	0	0	**0**	0	0	0	**0**	**0**

PLA	3	2	3	**8**	5	0	9	**14**	**22**
PLB	3	3	1	**7**	1	0	13	**14**	**21**
RR	13	9	11	**33**	3	3	30	**36**	**69**
SB	0	1	3	**4**	0	0	0	**0**	**4**
SBB	3	0	2	**5**					**5**
SK					2	1	5	**8**	**8**
WC	0	3	3	**6**	1	0	4	**5**	**11**
WP					1	0	3	**4**	**4**
Total	**40**	**30**	**80**	**150**	**41**	**21**	**139**	**204**	**354**

Table 6. Number of unique individual redbelly snakes marked in Ottawa (ON) and Gatineau (QC), Canada. Snakes marked in 2020 were captured between 23 June and 18 October, and snakes marked in 2021 were captured between 18 May and 1 October. Number of adult female (#F), adult male (#M), and juvenile, or snakes for which sex could not be determined (#J / U) are presented for each site in each year. Totals per site, per year, and per age/sex category are also presented. Blank cells indicate sites that were not visited in that year.

	2020				2021				Both Years
Site	# F	# M	# J / U	**Total**	# F	# M	# J/U	**Total**	**Total**
BP	6	1	42	**49**					**49**
CC	2	0	6	**8**	0	0	1	**1**	**9**
CT					2	0	16	**18**	**18**
DD					0	0	0	**0**	**0**
GB					1	0	9	**10**	**10**
GLA					0	0	0	**0**	**0**
GLB					0	0	0	**0**	**0**
GP	0	0	2	**2**	0	0	24	**24**	**26**
KM					0	0	0	**0**	**0**
LV	1	0	7	**8**	0	0	1	**1**	**9**
MB	5	0	31	**36**	3	0	33	**36**	**72**
N51	2	0	2	**4**	0	0	0	**0**	**4**
P15	0	0	1	**1**	0	0	11	**11**	**12**
P16	2	2	58	**62**	6	4	59	**69**	**131**
P16B	0	0	15	**15**					**15**
P17	5	0	3	**8**	1	0	8	**9**	**17**
P3					0	0	19	**19**	**19**
P5	2	0	8	**10**	0	0	9	**9**	**19**
P8	0	0	0	**0**	2	0	18	**20**	**20**
PH	1	0	2	**3**	0	0	10	**10**	**13**

PLA	2	0	16	**18**	4	0	13	**17**	**35**
PLB	0	3	27	**30**	0	0	25	**25**	**55**
RR	0	0	1	**1**	0	0	0	**0**	**1**
SB	0	0	0	**0**	0	0	0	**0**	**0**
SBB	0	0	0	**0**					**0**
SK					0	1	17	**18**	**18**
WC	5	2	66	**73**	1	0	37	**38**	**111**
WP					1	1	26	**28**	28
Total	**33**	**8**	**287**	**328**	**21**	**6**	**340**	**363**	**691**

Table 7. Summary statistics for general linear mixed models of number of individual garter and redbelly snakes captured, and mean SVL for both species. Continuous predictor variables were scaled. Dependent variables tested were number of garter or redbelly snakes at each site, and mean SVL of garter or redbelly snakes at each site. Significant (≤0.05) p-values are in bold.

Model: Garter Snake Count

Variable	Estimate	p-value
Intercept	-2.94	**>0.001**
Road 500	-0.46	**0.04**
Field 1000	-0.35	0.08
Water 900	0.39	0.08
Date	-0.16	**0.01**
Temp	0.00	0.94
Time	0.52	**>0.001**
Boards	0.90	**0.03**
Mowed	-0.83	0.07

Model: Redbelly Snake Count

Variable	Estimate	p-value
Intercept	-2.48	**>0.001**
Urban 100	-1.31	**0.01**
Sides 600	-0.23	0.54
Field 200	0.12	0.65
Water 900	0.00	1.00
Date	-0.23	**>0.001**
Temp	-0.34	**>0.001**
Time	0.53	**>0.001**
Boards	0.84	**0.01**
Mowed	-0.47	0.42

Model: Gartner Snake SVL

Variable	Estimate	p-value
Intercept	47.36	**>0.001**
Urban 300	2.63	0.08
Field 200	-0.17	0.88
Water 600	0.76	0.46
Date	1.3	0.28
Temperature	3.36	**0.004**
Time	-1.15	0.21

Boards	-8.54	**0.05**
Mowed	1.38	0.61

Model: Redbelly Snake SVL		
Variable	Estimate	p-value
Intercept	12.15	**0.002**
Road 300	1.17	0.18
Sides 300	0.48	0.63
Field 900	1.22	0.17
Water 800	1.05	0.22
Forest 200	1.8	0.1
Date	0.1	0.82
Temperature	1.69	**>0.001**
Time	-0.37	0.29
Boards	1.54	0.35
Mowed	0.4	0.75

FIGURES

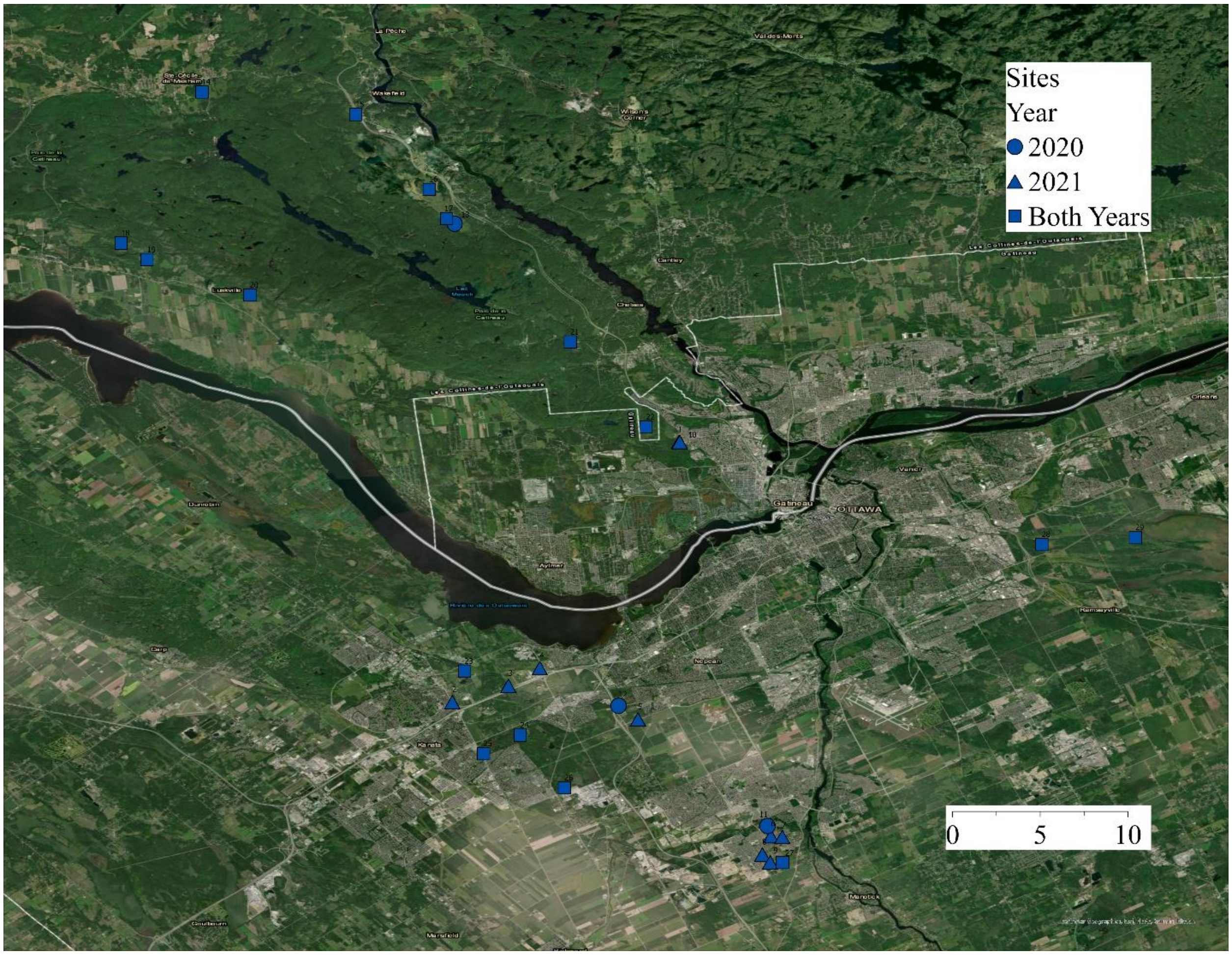


Figure 1. Map of field sites in the Ottawa/Gatineau (Ontario/Quebec, Canada) area. Sites visited in 2020 only are labelled with circles, sites visited in 2021 only are labelled with triangles, and sites visited in both 2020 and 2021 are labelled with squares. Scale bar represents 10 kilometres.

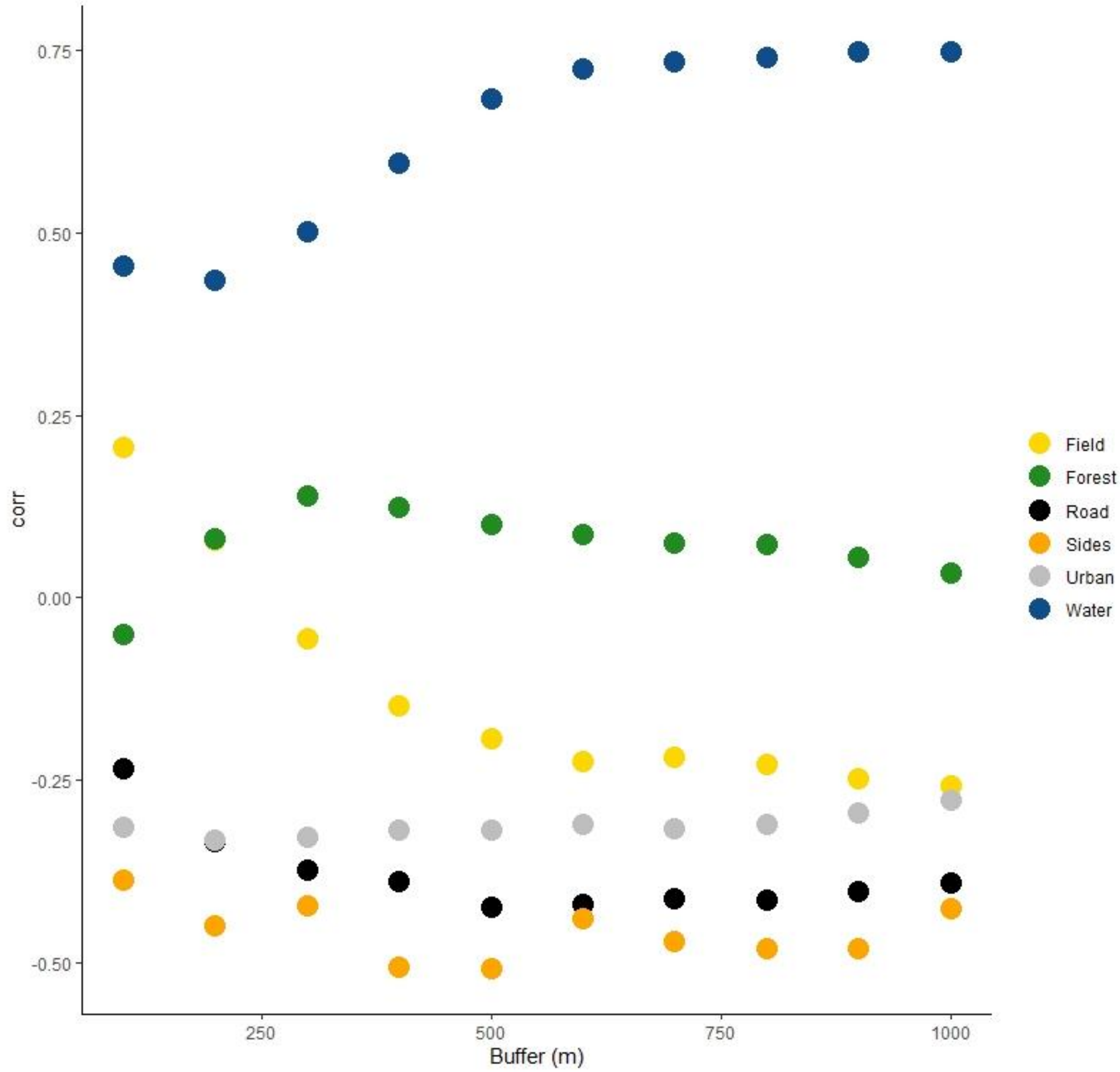


Figure 2. Pearson's correlation of habitat variables with number of individual garter snakes. Correlation of continuous variables (field, forest, road, urban, and water) and sides are displayed over distances from 100-1000 m in 100 m increments.

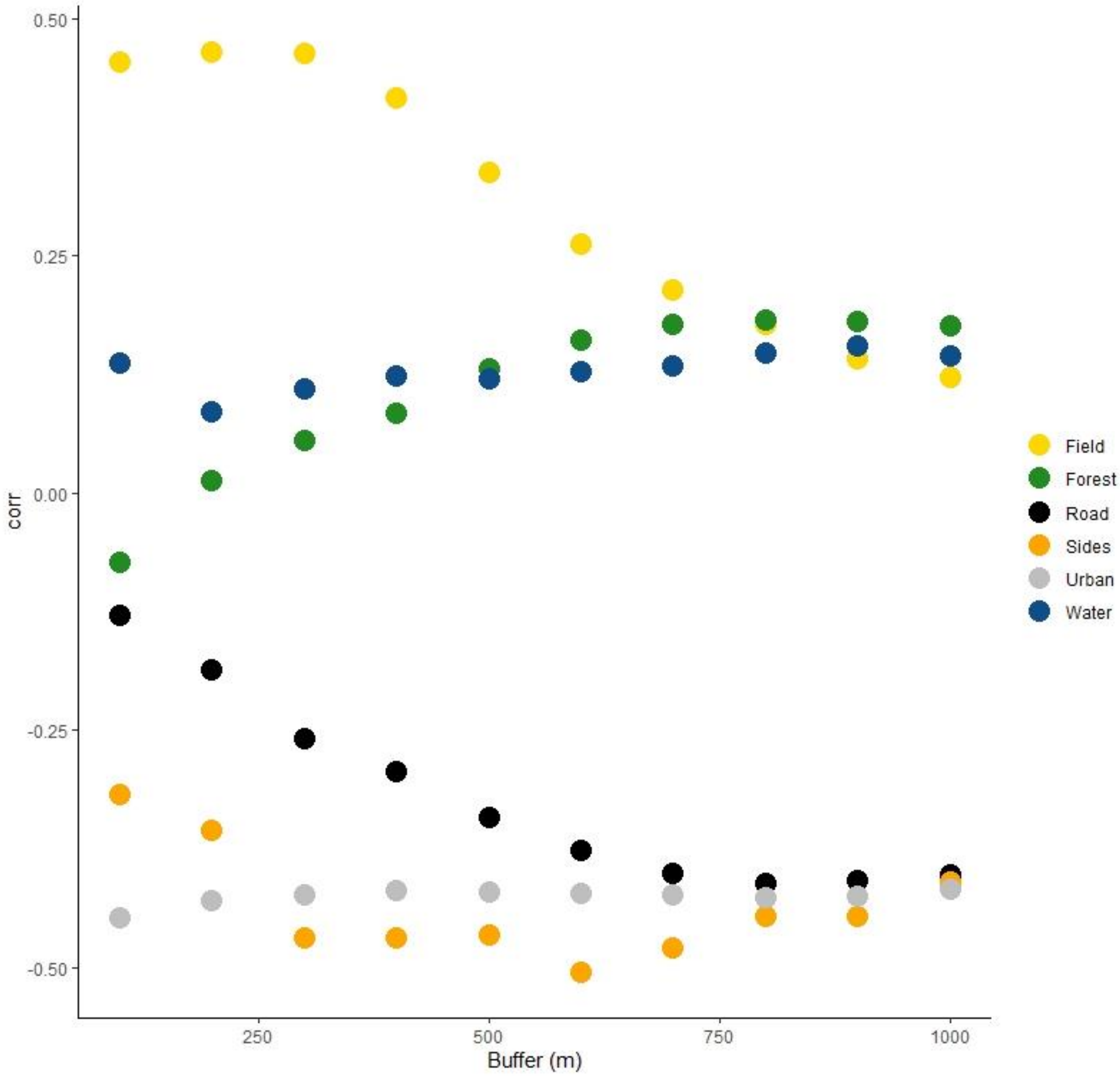


Figure 3. Pearson's correlation of habitat variables with number of individual redbelly snakes. Correlation of continuous variables (field, forest, road, urban, and water) and sides are displayed over distances from 100-1000 m in 100 m increments.

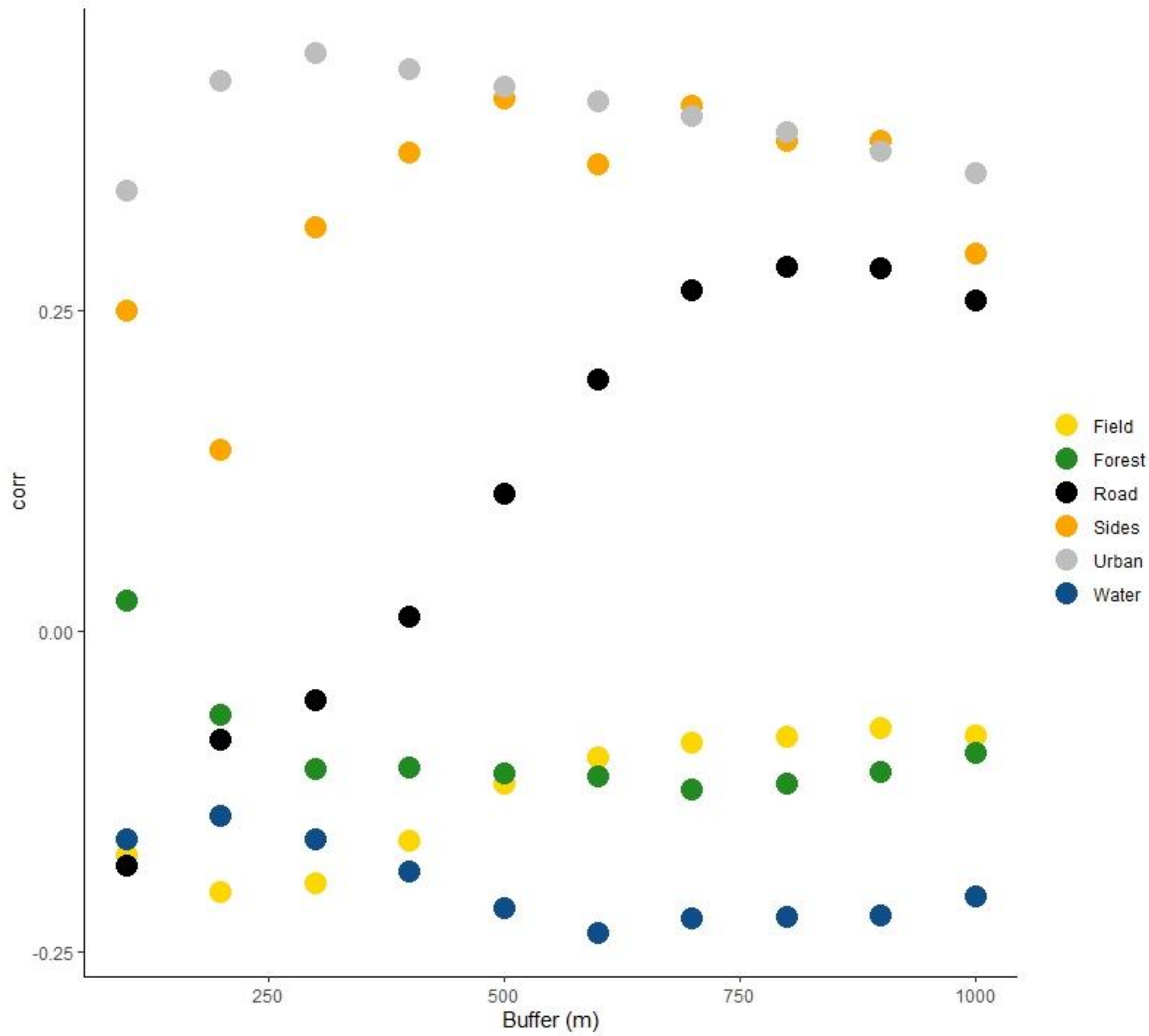


Figure 4. Pearson's correlation of habitat variables with number of mean SVL of garter snakes. Correlation of continuous variables (field, forest, road, urban, and water) and sides are displayed over distances from 100-1000 m in 100 m increments.

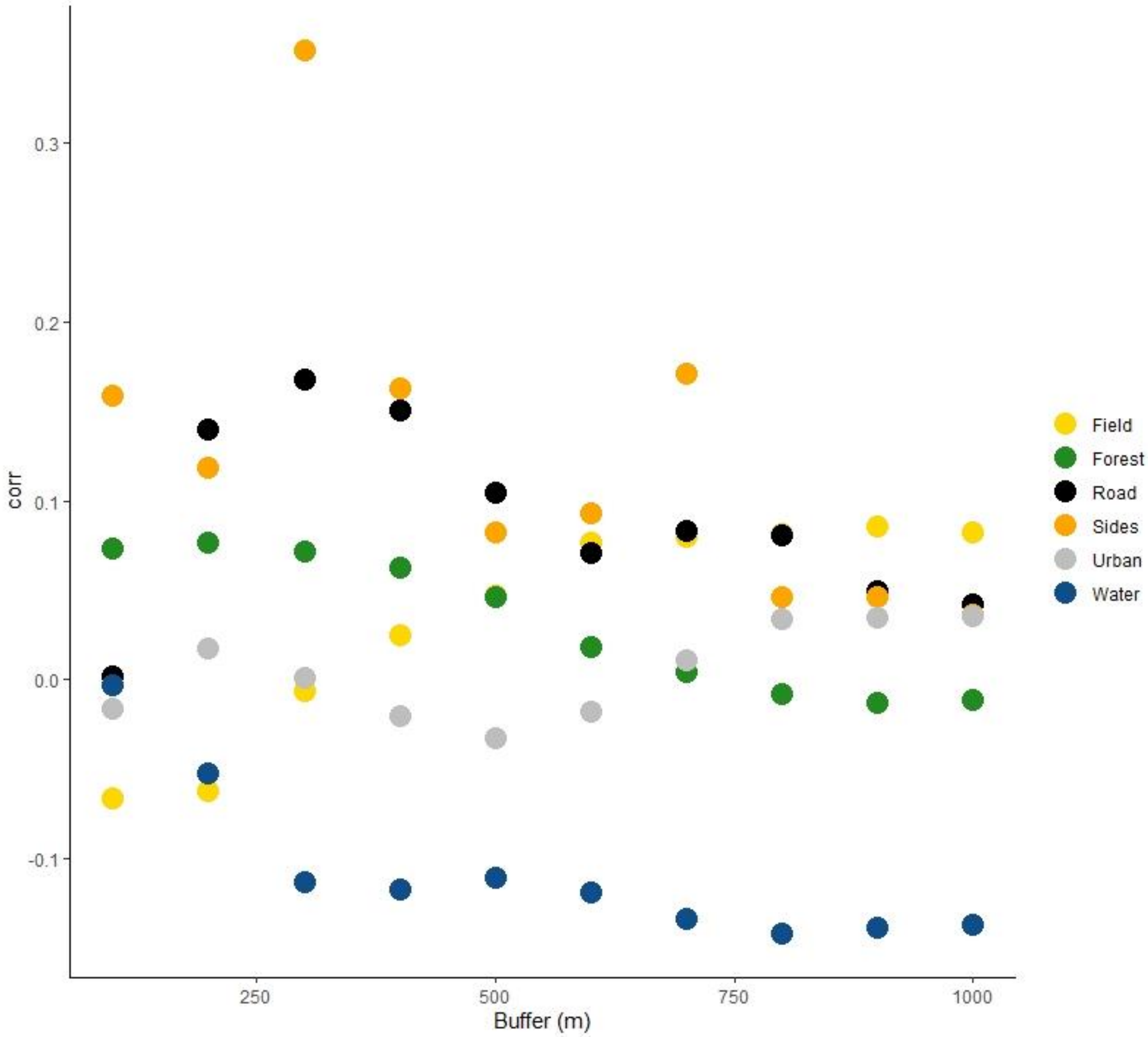


Figure 5. Pearson's correlation of habitat variables with mean SVL of redbelly snakes. Correlation of continuous variables (field, forest, road, urban, and water) and sides are displayed over distances from 100-1000 m in 100 m increments.

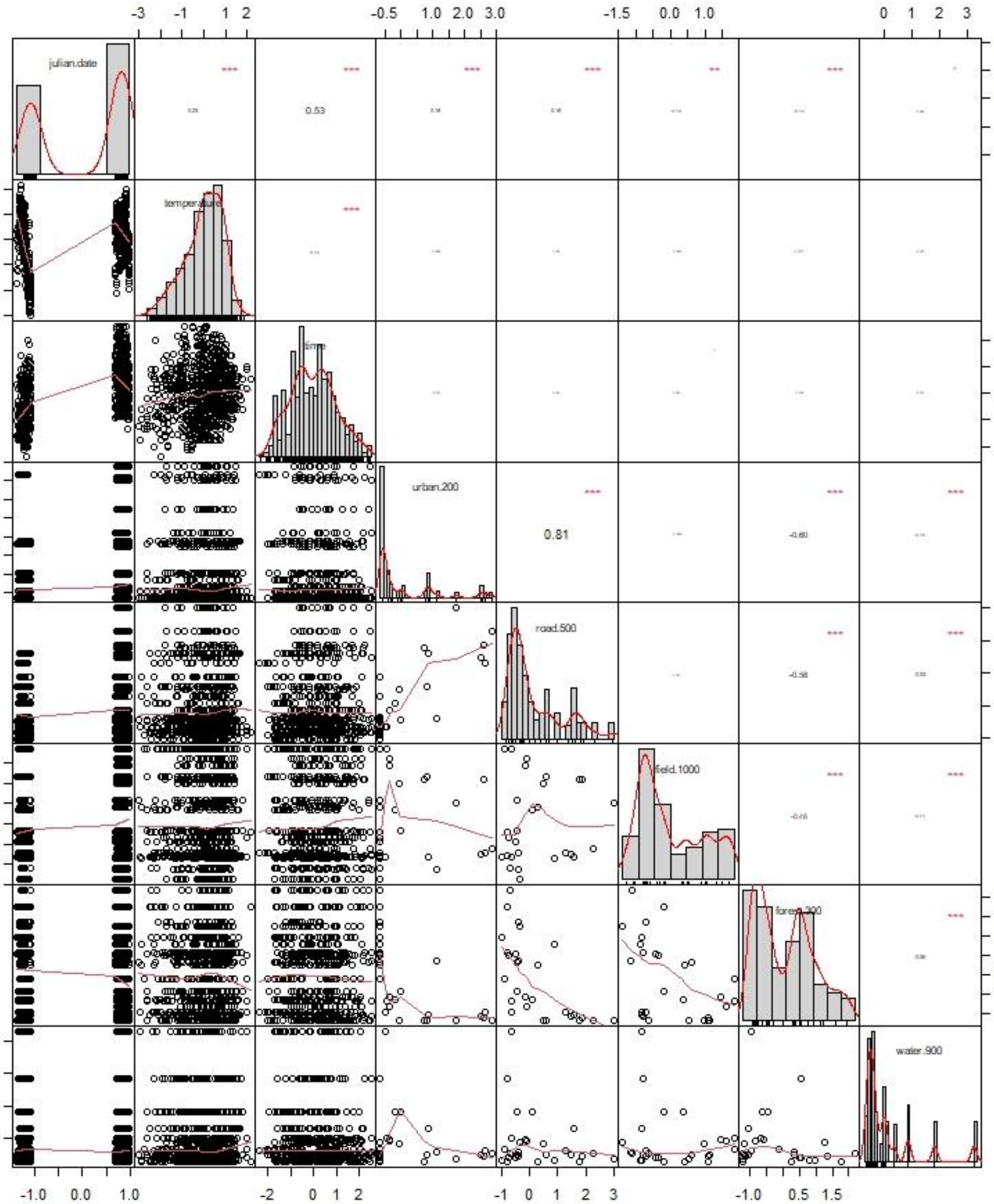


Figure 6. Correlation matrix of continuous predictor variables used to model number of garter snakes. Correlation ≥ 0.7 is considered high. Asterisks represent p-values (*** = 0.001, ** = 0.01, * = 0.05).

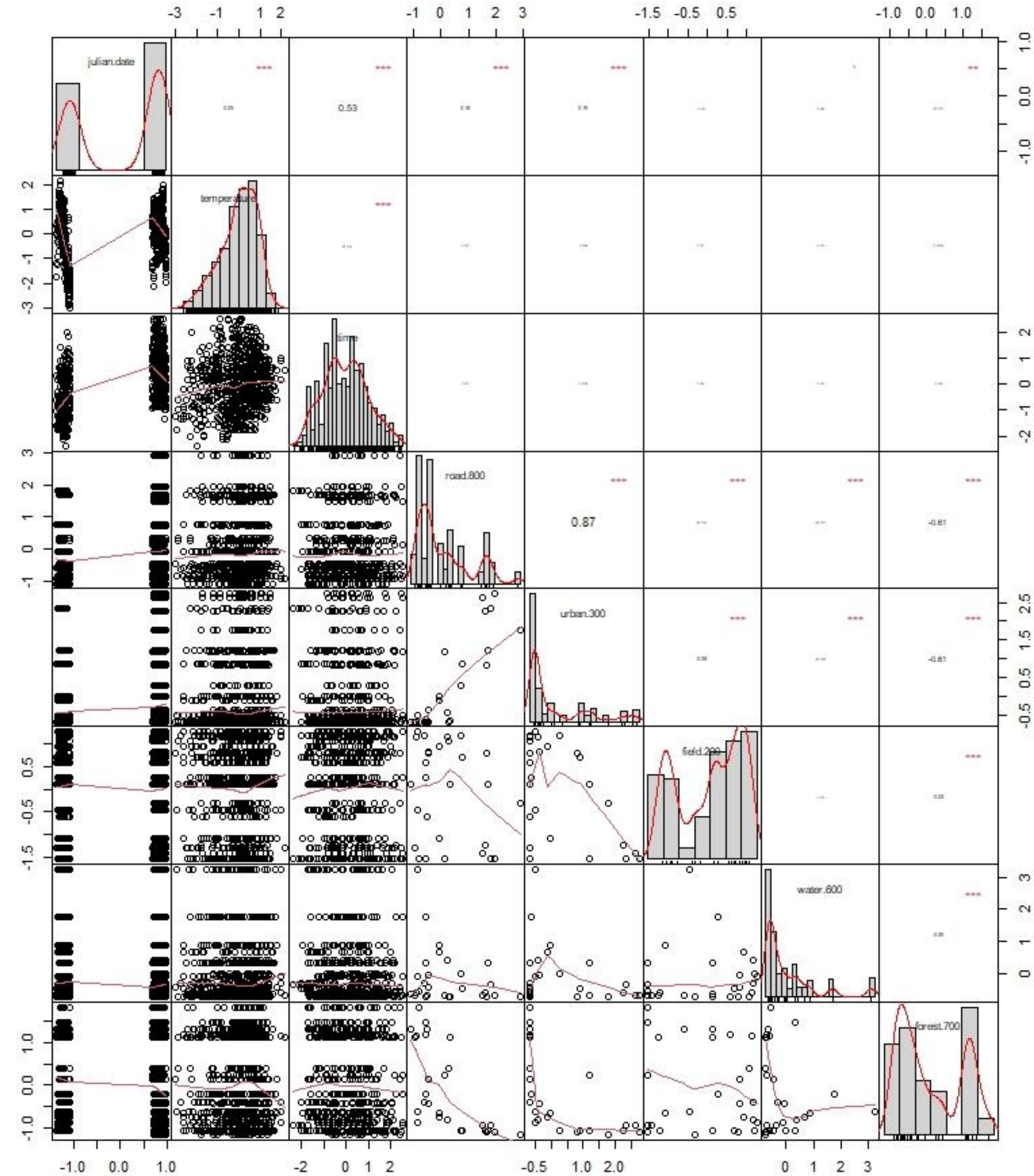


Figure 7. Correlation matrix of continuous predictor variables used to model SVL of garter snakes. Correlation ≥ 0.7 is considered high. Asterisks represent p-values (*** = 0.001, ** = 0.01, * = 0.05).

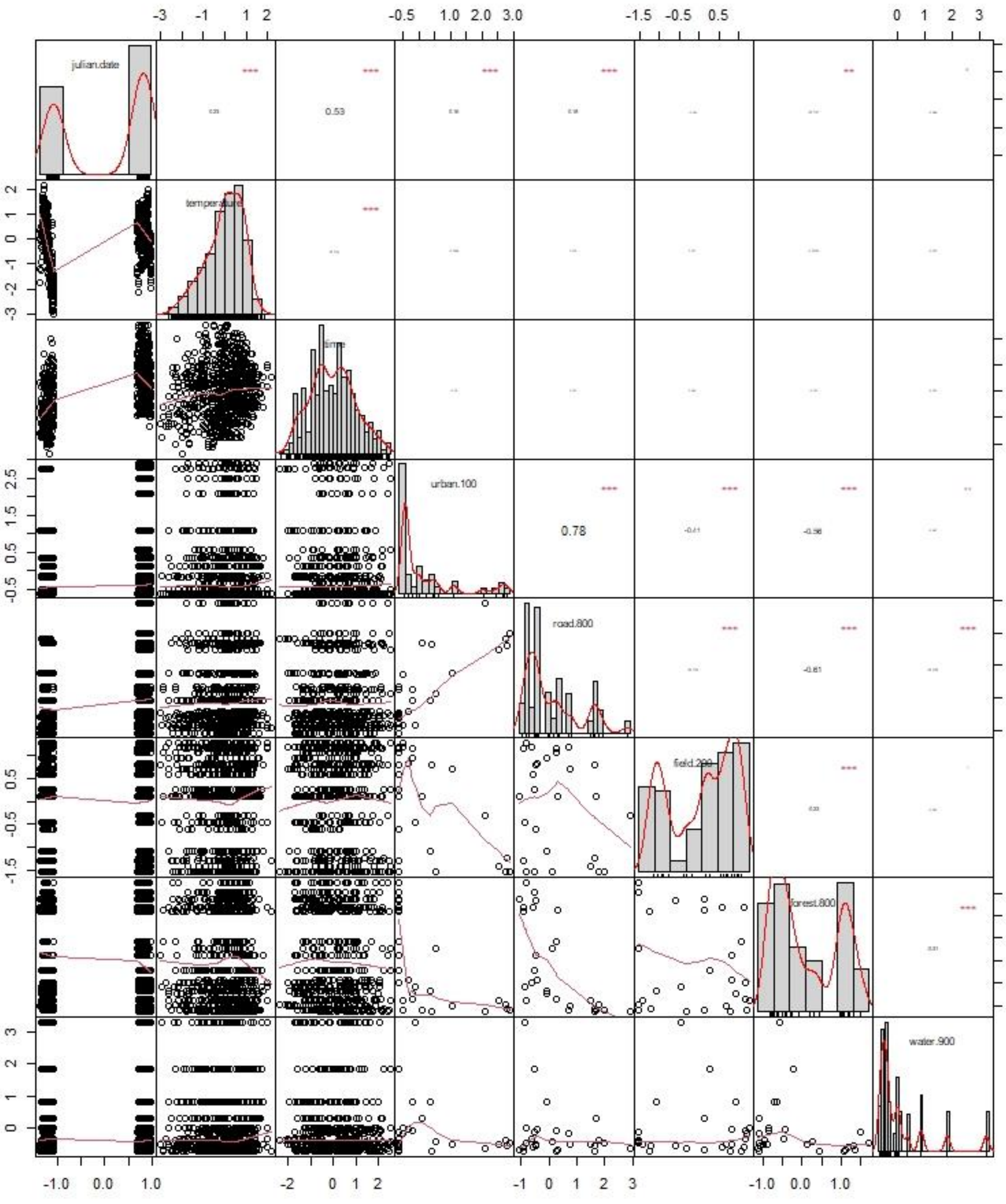


Figure 8. Correlation matrix of continuous predictor variables used to model number of redbelly snakes. Correlation ≥ 0.7 is considered high. Asterisks represent p-values (*** = 0.001, ** = 0.01, * = 0.05).

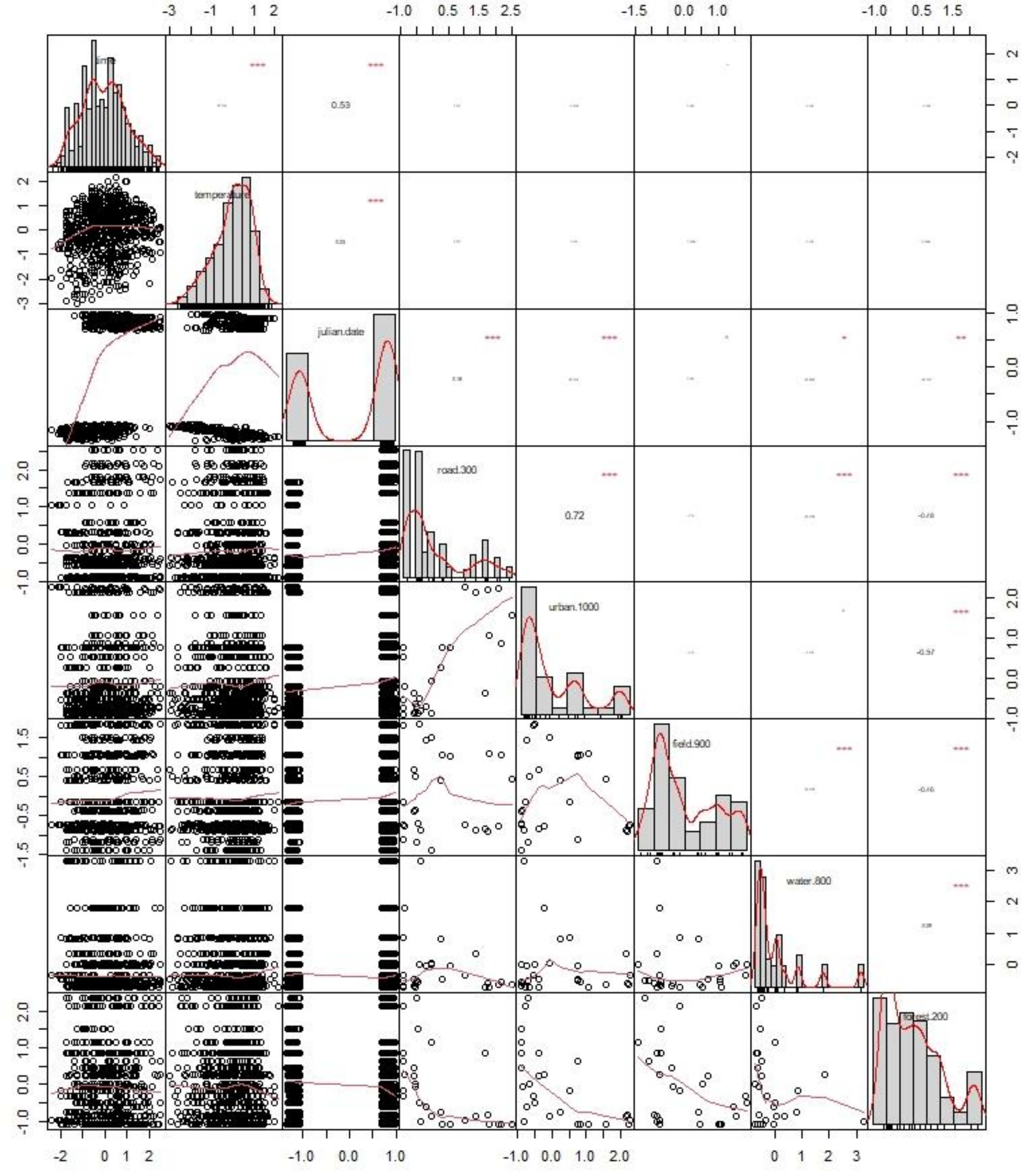


Figure 9. Correlation matrix of continuous predictor variables used to model SVL of redbelly snakes. Correlation ≥ 0.7 is considered high. Asterisks represent p-values (*** = 0.001, ** = 0.01, * = 0.05).

SUPPLEMENTS

Supplement 1: Population Size Estimate

Because the capture rates for both species were low at most sites (Tables 6, 7), capture-mark-recapture models could not be used to estimate population size reliably at all sites. Instead, I standardized the number of individual snakes captured at each site for sampling effort (total number of visits over the two survey periods and number of boards installed per site). This standardized number of individuals captured was used as a proxy for population size of each species at each site.

To confirm that the number of unique individuals captured per site is a suitable proxy for population size, I used a POPAN formulation of a Jolly-Seber (JS) mark recapture model (Jolly 1965; Seber 1965; Arnason and Schwarz 1995) to estimate population size for the six sites with sufficient data (≥20 marked individuals and ≥10% recapture rate). Because only one site had sufficient captures and recaptures of garter snakes, this analysis was only performed for redbelly snake population size. The model was constructed using Program MARK version 9.0 (White and Burnham 1999). The number of weeks each site was visited, and the interval between the last visit in 2020 and first visit in 2021 were included in the model. The parameters were constant probability of capture [p(.)], constant probability of survival [φ(.)], and time dependent probability of entry into the population [pent(t)]. The parameter specific link functions used were Logit for apparent survival (φ) and capture probability (p), MLogit for probability of entry into the population (pent), and Log for initial population size (N) (Supplemental Table 1).

I then followed the procedure of identifying the scale of maximum effect as outlined in “Results”. I was not able to perform stepwise AIC in both directions as I had too few sites and too many variables for the full model to run, and instead performed stepwise AIC forward with the starting null model redbelly.snake.population.estimate~1. The final model derived by AIC included the variable “fields” (Supplemental Table 2). Given the small sample size, it is unsurprising that a model consisting of more than one variable was not selected by AIC. Field was not significant in the model (Supplemental Table 3). Again, because the sample size was small, it is unsurprising that I was not able to detect a statistically significant effect. Field is negatively correlated with estimated redbelly population (Supplemental Figure 1), while it was positively correlated with number of redbelly snakes. I cannot make any conclusions about whether the number of unique individuals is a suitable proxy for a mark recapture estimate of population size.

Supplemental Table 1. Population size estimates for redbelly snakes at six sites in Gatineau and Ottawa. Estimates and 95% CI were derived from a POPAN JS model of capture and recapture data. The sites included represent the only six sites where I captured and recaptured snakes above the minimum threshold (see text).

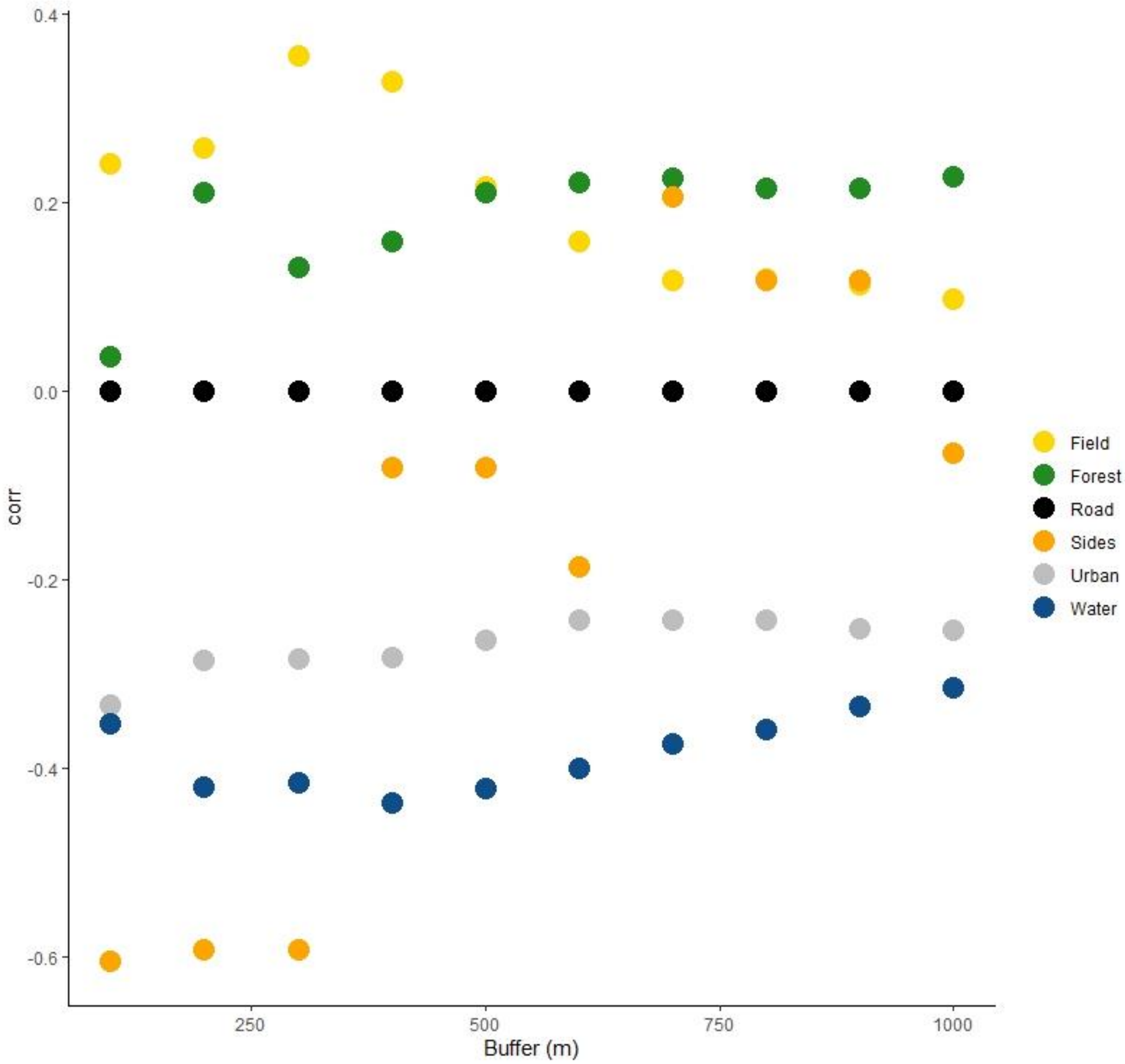
Site	Population Size Estimate (95% CI)
BP	230 (113, 469)
MB	251 (162, 390)
P8	141 (38, 519)
P16	1264 (675, 2365)
PLB	187 (107, 327)
WC	455 (308, 671)

Supplemental Table 2. Model selection for estimated population of redbelly snakes. AIC was performed forwards, with the starting model redbelly.population~1 (a null model).

Step	AIC
Null Model	26.9
+ Fields	26

Supplemental Table 3. Results of final GLM for estimated redbelly population. Estimated redbelly population ~ field was the best model as determined by AIC. The estimate, standard error, and p-value for each coefficient in the model are presented. Significant p-values (<0.05) are in bold.

Coefficient	Estimate	Standard Error	p-value
Intercept	18.9	3.1	**0.003**
Field	-5.4	3.4	0.2



Supplemental Figure 1. Pearson's correlation of habitat variables with number of estimated population size of redbelly snakes. Correlation of continuous variables (field, forest, road, urban, and water) and sides are displayed over distances from 100-1000 m in 100 m increments.