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Article

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 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. We studied the impact of road density on abundance of two snake species: redbelly snakes (*Storeria occipitomaculata* Storer, 1839) and garter snakes (*Thamnophis sirtalis* Linnaeus, 1758) around Ottawa, Canada. We hypothesized that roads are detrimental to snake populations due to road avoidance and mortality. Therefore, we predicted that snakes should be less abundant at sites with higher road density in their surroundings. We deployed cover boards at 28 sites along a gradient of road density in 2020 and 2021. We visited sites weekly, counted the number of individuals of both species, and measured snout–vent length (SVL) of all individuals captured. We captured fewer garter snakes at sites surrounded by more roads and fewer redbelly snakes at sites surrounded by more urban habitat. Snakes at sites surrounded by more roads were not smaller. The effects of roads and urbanization on the number of snakes were modest, but indicate decreasing population sizes that could lead to loss of ecological function.

Key words: anthropogenic land use, road ecology, garter snake, *Thamnophis sirtalis*, redbelly snake, *Storeria occipitomaculata*

1 Introduction

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). Anthropogenic land use includes 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). 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 is reduced following the construction of the road (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). 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). In snakes, small species are more likely to avoid crossing roads than large species (Andrews and Gibbons 2005). 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 fragmented landscapes, 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 abundances irrespective of phylogeny or climate, making it the strongest predictor of species- and population-level extinction for reptiles (Doherty et al. 2020). Reptiles, 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 to regulate their body temperatures (Blouin-Demers and Weatherhead 2001), 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). 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 also move slowly which increases their exposure time on the road surface and likelihood of being struck by a vehicle (Ashley and Robinson 1996; Rudolph et al. 1998; Rytwinski and Fahrig 2015; Choquette and Valliant 2016). Substantial snake mortality has been documented following the construction of a road (Evans et al. 2011). There is even evidence 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 has been demonstrated in snakes (Andrews and Gibbons 2005; Robson and Blouin-Demers 2013; Paterson et al. 2019) and inferred by decreasing population density in areas in proximity to a road (Patrick and Gibbs 2009). The impact of anthropogenic disturbance on habitat fragmentation and population isolation of snakes is variable. For example, eastern massasauga rattlesnakes (*Sistrurus catenatus* Rafinesque, 1818) already had low gene flow between populations prior to major alteration of their habitat by humans (Chiucchi and Gibbs 2010), whereas populations of plains garter snakes (*Thamnophis radix* Baird and Girard, 1853) are more isolated and have reduced genetic diversity in urbanized areas (Gangloff et al. 2017), while timber rattlesnakes (*Crotalus horridus* Linnaeus, 1758) have reduced gene flow between populations separated by roads (Clark et al. 2010).

Common garter snakes (*Thamnophis sirtalis* Linnaeus, 1758) and redbelly snakes (*Storeria occipitomaculata* Storer, 1839) 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. Our objective was to determine whether the 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) depends on road density in the surrounding area. For all the reasons above, we hypothesized that roads are detrimental to snakes. Therefore, we predicted that there would be fewer snakes at sites surrounded by more roads. We also hypothesized that road mortality prevents snakes from reaching their full size. Thus, we predicted that snakes at sites surrounded by more roads would be smaller.

2 Materials and methods

2.1 Study sites and species

Redbelly snakes (*Storeria occipitomaculata*) are <30 cm, while garter snakes (*Thamnophis sirtalis*) are up to ~50 cm. Both snakes are locally abundant in eastern Ontario and southern Québec (Canada) and commonly found in old fields (Carpenter 1952; Halliday and Blouin-Demers 2015, 2016; Retamal Diaz and Blouin-Demers 2017).

We selected 28 sites around Gatineau (Québec, Canada) and Ottawa (Ontario, Canada) to obtain a gradient of road density (Fig. 1). All sites were within 50 km of one another. Of these 28 sites, we visited three in 2020 only, nine in 2021 only, and sixteen in both years (Fig. 1, Supplemental Table S1). All sites were old fields (field habitats not currently in use for agriculture), the preferred habitat for 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 bluegrasses (*Poa* spp L.), timothies (*Phleum* spp L.), and forbs (mainly goldenrod (*Solidago* spp L.) and clover (*Trifolium* spp L.))). This research was conducted with an Ontario Wildlife Scientific Collector's Authorization (permit numbers 1095471, 1097449) and Permis Scientifique du Québec (permit numbers 20-07-SF-004-GR-0, 21-07-SF-001-GR-0), and approved by the University of Ottawa's Animal Care Committee in accordance with the Canadian Council on Animal Care (protocol number BL-3293).

2.2 Field surveys

At each site, we installed 10–30 plywood cover boards (60 × 60 × 1.27 cm) along 200–600 m transects with cover boards spaced 20 m apart (Carpenter 1952; Kjoss and Litvaitis 2001; Halliday and Blouin-Demers 2015). We visited each site approximately once per week between 23 June and 18 October in 2020, and between 18 May and 1 October in 2021 (Supplemental Table S1). We visited sites under favourable weather conditions (i.e., clear skies and air temperature between 10 °C and 30 °C).

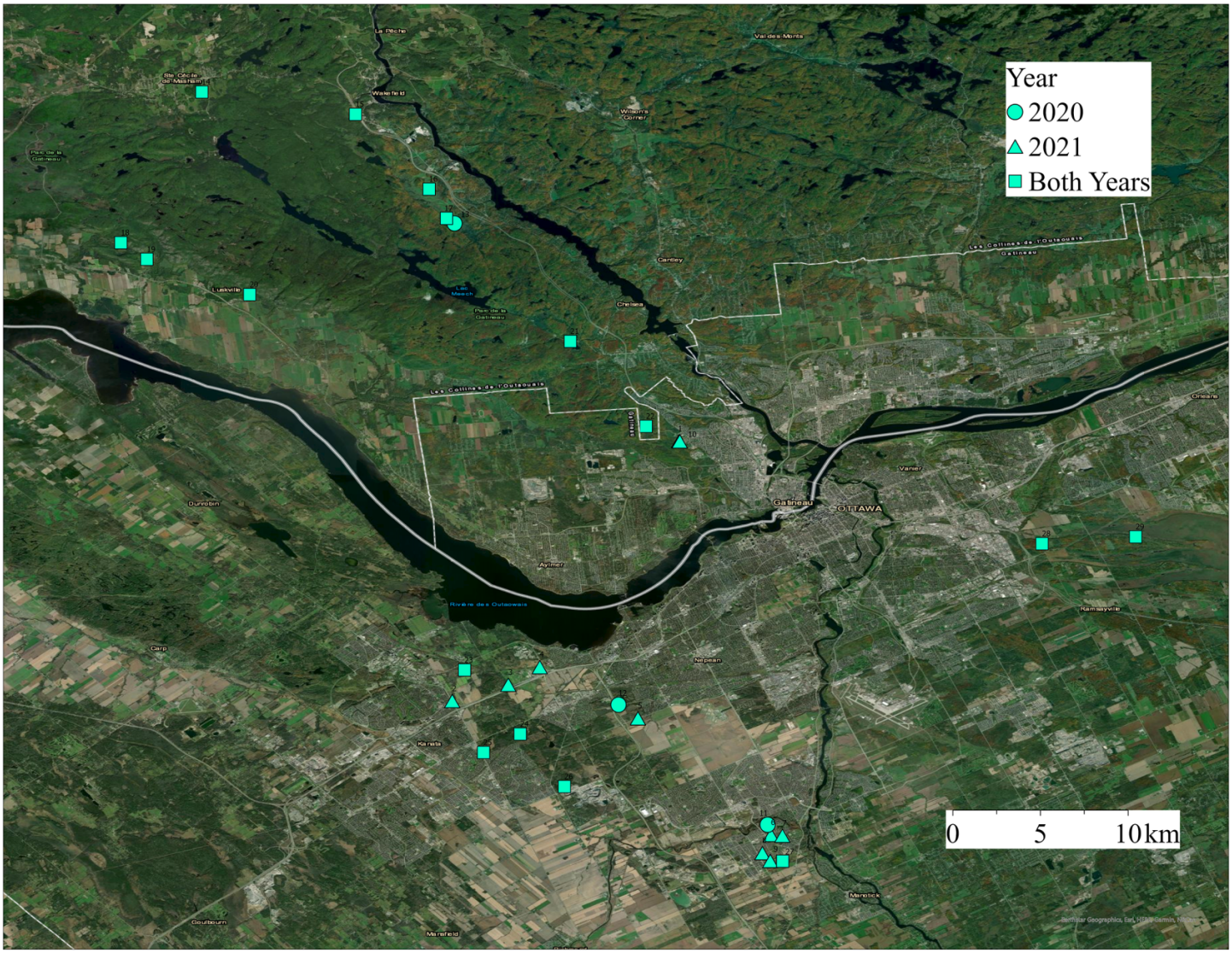
During each visit, one to three people walked the transect at a distance of 2 m from one another at a constant pace (Carpenter 1952; Halliday and Blouin-Demers 2015). Each cover board was overturned and any snakes found under the board were captured. Snakes encountered between boards while walking the transect were also captured, but this represented very few snakes (see "Results" section). Snakes were measured from the tip of the snout to the cloacal opening (snout–vent length: SVL). The date, time, and location of each capture were recorded using a Garmin GPSMap 76s handheld device (Garmin, Olathe, Kansas, USA). Air temperature and weather conditions were obtained from the Government of Canada records taken at the Ottawa International Airport situated 8–44 km from our study sites. Snakes that had not previously been captured were uniquely marked by branding on the ventral scales anterior to the cloaca following Winne et al. (2006).

We standardized the number of unique individual snakes captured at each site by dividing by the number of visits per site and the number of cover boards deployed. We had too few recaptures at most sites (0/1 to 25/111, mean of 6% recapture rate for garter snakes and 11% recapture rate for redbelly snakes) to allow precise capture–mark–recapture estimations of population size at each site (Gigeroff 2022). The number of unique individual snakes captured was square-root transformed for both species.

2.3 Habitat variables

We considered seven habitat variables for modelling: road density (km road/km^2 area), 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. We derived percent cover of the four habitat types from the Ontario Land

Fig. 1. Map of field sites in the Ottawa/Gatineau (Ontario/Québec, 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 km. The base map is World Boundaries and Places provided by ArcGIS Map Service with map sources Earthstar Geographics, Esri, HERE, Garmin, and NRCan. Data plotted are shapefile data of field site locations. Map projection is NAD83.



Cover Compilation Version 2.0 (OLCC) and the Comptes des Terres du Québec (CTQ). We combined the 29 land cover categories for OLCC and 11 land cover categories for CTQ into the four categories outlined above, and merged the two land cover data sets using ArcGIS Pro Version 2.7.3 (Esri 2020). The old fields used as study sites were recorded as agricultural fields in the CTQ data set, and agriculture or undifferentiated rural land in the OLCC data set, so both these land classes were categorized as "fields". Road density was derived from the 2020 Canada Road Network downloaded from Statistics Canada (Statistics Canada 2020).

We constructed buffers around each site in 100 m increments from 100 to 1000 m using ArcGIS Pro. Both garter and redbelly snakes can travel approximately 500 m (Blanchard 1937; Carpenter 1952), so we chose 1000 m as the maximum buffer distance to ensure that we included the appropriate area that snakes of both species are likely to experience in a season (Jackson and Fahrig 2015). This distance is also frequently used in studies of landscape effects in small vertebrates (Jackson and Fahrig 2015; Moraga et al. 2019). Because almost all snakes were captured under cover boards (see "Results" section), the cover board transects were used to centre the buffers. The area of each buffer (square kilometres) and total length of roads within buffers (kilometres) 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 ArcGIS Pro. We 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 given buffer. Whether a field was mowed was reported by Gatineau Park and Stonebridge Golf Club staff.

Continuous predictor variables were scaled using the scale function in R (R Core Team 2021). Mean SVL for both species did not deviate from normality based on the Shapiro–Wilk test (Garter: $W = 0.94$, $p = 0.26$; Redbelly: $W = 0.94$, $p = 0.21$), nor did the residuals deviate visually from normality. For 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 for habitat variables, we calculated Pearson's correlation coefficients between the standardized number of snakes and the habitat variables (ROADS, %FIELD, %FOREST, %URBAN, %WATER, and SIDES) at each buffer distance. 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). We repeated this process for SVL for both species.

2.4 Modelling

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 (count and SVL for both species). We also included Julian date, temperature, time of day, and number of boards at each site as control variables in the full models. We included site as a random effect.

We tested each full model for variance inflation using the gvif() function in the package "car" (Fox and Weisberg 2019). We removed any explanatory variables with gvif scores ≥ 2 from the final models (Supplemental Table S2). We removed the variables "%FOREST" and "SIDES" from the model for garter snake count, "%FOREST" from the model for redbelly snake count, "%FOREST", "ROADS", and "SIDES" from the model for garter snake SVL, and "%URBAN" from the model for redbelly snake SVL due to multicollinearity (Supplemental Table S2).

We performed a correlation analysis for the continuous predictor variables in all of the full models using the cor() function in R. We found high ($\geq$0.7) Pearson's correlations between "%URBAN" and "ROADS" at the scales used for all models (Supplemental Figs. S1 and S2).

Because "%URBAN" and "ROADS" were highly correlated at the scales used for modeling garter and redbelly snake counts, but were not removed from those models due to high gvif scores, we built candidate models with only one of those variables. We compared the fit of those candidate models using the Akaike information criterion (AIC) from the glmer() function in the "lme4" package in R (Bates et al. 2022).

3 Results

3.1 Snake surveys

In total, we captured 691 individual redbelly snakes 801 times, and 354 individual garter snakes 386 times (Supplemental Tables S3 and S4). Of those captures, 83% of garter snakes and 99% of redbelly snakes were captured under cover boards.

Most redbelly snakes were captured once (604 individuals, 87% of the sample), 66 individuals were captured twice (10%), 16 individuals (3%) were captured thrice, 3 individuals were captured four 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% of the sample), 27 individuals (6%) were captured twice, and 3 individuals (0.3%) were captured thrice. Four individuals were captured in both 2020 and 2021, 146 individuals were captured only in 2020, and 204 individuals were captured only in 2021.

3.2 Predictors of snake density

The scale of maximum effect varied from 200 to 1000 m for number of garter snakes, 200 to 900 m for number of redbelly snakes, 200 to 800 m for mean SVL of garter snakes, and 200 to 1000 m for mean SVL of redbelly snakes (Supplemental Figs. S3–S6). The habitat variable that best predicted the number of garter snakes was road density ($p = 0.04$, $z|_{769|} = -2.05$; Table 1). Time of year ($p = 0.01$, $z_{|769|} = -2.43$), time of day ($p < 0.001$, $z_{|769|} = 9.12$), and number of boards ($p = 0.03$, $z_{|769|} = 2.15$) at each site also had moderate, statistically significant effects on the number of garter snakes captured (Table 1). We found more garter snakes at sites surrounded by fewer roads, and more garter snakes earlier in the year, later in the day, and at sites with more boards (Fig. 2*a*, Supplemental Fig. S7).

The habitat variable that best predicted the number of redbelly snakes was urban area ($p = 0.001$, $z_{|768|} = -2.6$; Table 1). Time of year ($p < 0.001$, $z_{|768|} = -4.79$), time of day (p value < 0.001, $z_{|768|} = 13.06$), number of boards at each site ($p = 0.01$, $z_{|768|} = 2.45$), and temperature ($p < 0.001$, $z_{|768|} = -9.84$) also had moderate, statistically significant effects on the number of redbelly snakes captured (Table 1). We 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, and when the temperature was cooler (Fig. 2*b*, Supplemental Fig. S8).

No habitat variables were statistically significant in predicting the size of either species. Temperature ($p = 0.003$, $t_{|157.93|} = 2.96$) and number of boards ($p = 0.46$, $t_{|6.04|} = -2.49$) had moderate, statistically significant effects on the size of garter snakes captured (Table 1). We found larger garter snakes on warmer days and at sites with fewer boards (Supplemental Fig. S9). Temperature also had a moderate, statistically significant effect on the size of redbelly snakes ($p < 0.001$, $t_{|222.09|} = 4.6$; Table 1). We found larger redbelly snakes on warmer days (Supplemental Fig. S10).

4 Discussion

4.1 What is the relationship between road density and snake abundance?

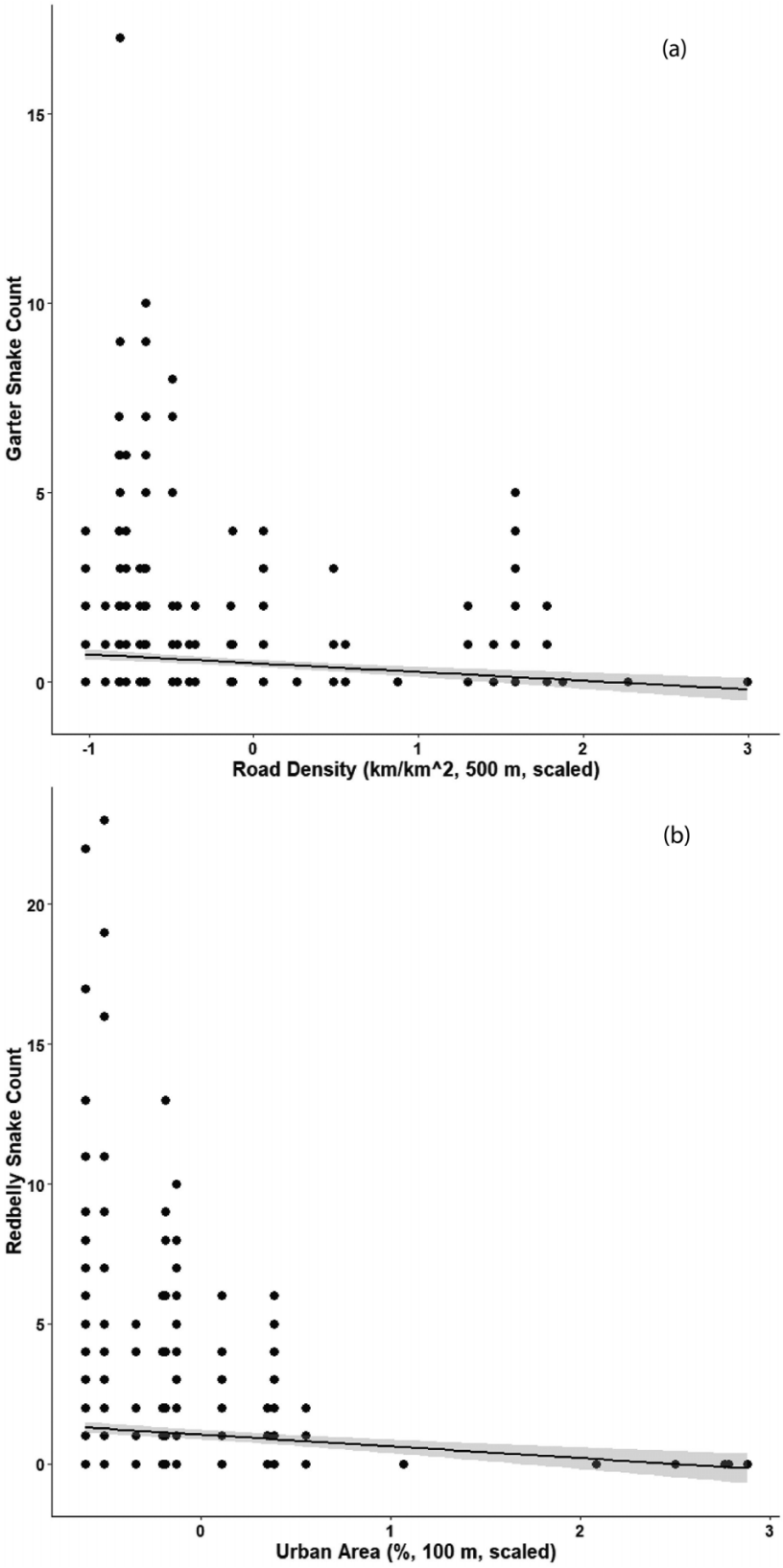
There may be fewer garter and redbelly snakes where there are more roads and urban areas because many snakes are killed on roads. Snakes comprise a large portion of road-

Table 1. Summary statistics for general linear models of number of individual garter (*Thamnophis sirtalis*) and redbelly snakes (*Storeria occipitomaculata*) captured, and mean SVL.

Model: Garter snake count					
Variable	Estimate	Standard error	Test statistic (*z*-score)	*p* value	df (residuals)
					769
Intercept	−2.94	0.86	−3.43	<0.001	
Road 500	−0.46	0.22	−2.05	0.04	
Field 1000	−0.35	0.2	−1.73	0.08	
Water 900	0.39	0.22	1.77	0.08	
Date	−0.16	0.06	−2.43	0.01	
Temp	0.00	0.05	0.08	0.94	
Time	0.52	0.06	9.12	<0.001	
Boards	0.90	0.04	2.15	0.03	
Mowed	−0.83	0.46	−1.8	0.07	
Model: Redbelly snake count					
Variable	Estimate	Standard error	Test statistic (*z*-score)	*p* value	df (residuals)
					768
Intercept	−2.48	0.75	−3.31	<0.001	
Urban 100	−1.31	0.5	−2.6	0.01	
Sides 600	−0.23	0.37	−0.61	0.54	
Field 200	0.12	0.26	0.45	0.65	
Water 900	0.00	0.27	0	1.00	
Date	−0.23	0.05	−4.79	<0.001	
Temp	−0.34	0.03	−9.84	<0.001	
Time	0.53	0.04	13.06	<0.001	
Boards	0.84	0.03	2.45	0.01	
Mowed	−0.47	0.58	−0.81	0.42	
Model: Garter snake SVL					
Variable	Estimate	Standard error	Test statistic (*t* value)	*p* value	df
Intercept	47.36	6.6	7.18	<0.001	5.66
Urban 300	2.63	1.4	1.88	0.08	12.6
Field 200	−0.17	1.07	−0.16	0.88	6.77
Water 600	0.76	0.88	0.87	0.46	2.39
Date	1.3	1.2	1.08	0.28	154.55
Temperature	3.36	1.13	2.96	0.004	157.93
Time	−1.15	0.91	−1.26	0.21	158.22
Boards	−8.54	0.34	−2.49	0.05	6.04
Mowed	1.38	2.62	0.53	0.61	9.4
Model: Redbelly snake SVL					
Variable	Estimate	Standard error	Test statistic (*t* value)	*p* value	df
Intercept	12.15	3.12	3.89	0.002	12.6
Road 300	1.17	0.8	1.46	0.18	8.91
Sides 300	0.48	0.96	0.5	0.63	9.24
Field 900	1.22	0.8	1.52	0.17	7.79
Water 800	1.05	0.78	1.35	0.22	7.31
Forest 200	1.8	0.99	1.82	0.1	8.48
Date	0.1	0.44	0.23	0.82	224.83
Temperature	1.69	0.37	4.6	<0.001	222.09
Time	−0.37	0.35	−1.05	0.29	227.78
Boards	1.54	0.16	0.97	0.35	13.27
Mowed	0.4	1.21	0.33	0.75	10.71

Note: Number of unique individual snakes was square-root transformed. Independent variables, except sides and mowed, were scaled. Numbers associated with habitat variables denote the buffer size used in the model in meters. 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.

Fig. 2. Relationships between the number of snakes captured around Gatineau, QC and Ottawa, ON in 2020 and 2021, and the best habitat variables predicted by our GLMMs. Regression lines and associated 95% confidence intervals are displayed. (*a*) shows the relationship between garter snake (*Thamnophis sirtalis*) count and road density within 500 m of our board transects and (*b*) shows the relationship between redbelly snake (*Storeria occipitomaculata*) count and percent urban area within 100 m of our board transects.



kill surveys (Ashley and Robinson 1996; Evans et al. 2011; Choquette and Valliant 2016), and increasing road density in an area may force snakes on to roads, especially during dispersal. If populations are reduced by numerous individuals being killed during dispersal (i.e., neonates), we would expect snakes to be larger where there are more roads, due to fewer neonates being captured. We did not find a statistically significant effect of roads on the size of garter or redbelly snakes, suggesting that dispersal is not a major source of road mortality for either species (Table 1).

Higher road density may indirectly impact garter and redbelly snakes occupancy by decreasing 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), used species occupancy from citizen science, and considered road type (paved vs. unpaved, average traffic speed), and anthropogenic land cover, while our study was undertaken in a smaller area (Gatineau and Ottawa), used abundance based on field surveys, grouped roads, and considered both anthropogenic and natural land cover types. It is possible that garter and redbelly snakes are found to be sensitive to anthropogenic disturbance when all road and habitat types are considered. Shepard et al. (2008) found that road mortality in eastern massasauga rattlesnakes increased with habitat quality. Higher quality habitat presumably can support more snakes, increasing the potential for road mortality.

We did not include road type in our models of snake abundance or size because of potential issues with including too many predictor variables given our number of sites. Whether or not a road is paved affects the likelihood of crossing by hognose snakes (*Heterodon platirhinos* Sonnini and Latreille, 1801), 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. Finally, paved roads are more prevalent in urban areas, while unpaved roads are more prevalent in rural areas. Higher percent cover of urban area reduced significantly the number of redbelly snakes captured.

Because abundance is a coarse population measure, roads may have effects on snake populations that we were 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. In addition, roads can have physiological impacts on snakes that were not measured in this study. For example, copperhead snakes (*Agkistrodon contortrix* Linnaeus, 1766) captured on roads exhibit a decreased stress response relative to snakes captured in forests (Owen et al. 2014).

4.2 What does this mean more broadly for snake populations?

Efforts are 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 underpasses 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 massassauga rattlesnakes (Colley et al. 2017), while grey rat snakes (*Pantherophis spiloides* A.M.C. Duméril, Bibron, and A.H.A. Duméril, 1854) are able to climb over certain types of fences (Macpherson et al. 2021), and common garter snakes are not always prevented from accessing roads by fencing (Boyle et al. 2021). The efficacy of underpasses or other taxon-specific ecopassages is also debated, because snakes sometimes ignore underpasses 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 mitigation structures are used, they may not be effective at preventing snake mortality if they are not designed and tested for a specific species. Interventions rarely, if ever, focus on mitigating other, sublethal effects of roads, such as road avoidance, and reduction in habitat quality surrounding roads and this constitutes a fruitful avenue for future research.

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Data availability

Data generated and analyzed during this study are available on the github repository, https://github.com/agigeroff/roads-affect-snakes.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2022-0127.

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