

Effect of landscape composition on snake abundance in wetlands

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Abstract

Habitat loss is driving the biodiversity loss crisis, and agriculture is one of the leading sources. Reptiles are especially sensitive to environmental change, yet are less frequently studied. My study aims to investigate the landscape effect of agriculture on garter snake (*Thamnophis sirtalis*) and redbelly snake (*Storeria occipitomaculata*) abundance in wetlands in Eastern Ontario and Southern Québec, Canada. I expected snakes to be less abundant at wetland sites with more agricultural land in the surrounding landscape. I also expected snakes to be smaller on average in wetlands in more agricultural landscapes. I tested this by estimating population abundance in wetlands embedded across a gradient of agricultural and natural landscapes in the Ottawa/Gatineau area. Sites were surveyed once a week from May to September in 2023 and 2024, and any snakes captured were counted, marked, and measured. The number of garter snakes and redbelly snakes caught did not differ significantly across sites with increasing agricultural land cover in the surrounding landscape, according to the final model; however, an alternative model indicated significantly fewer snakes in wetlands with more surrounding agriculture. Snake size did not significantly differ across the agricultural gradient.

Résumé

La perte d'habitat est à l'origine de la crise de la biodiversité et l'agriculture en est l'une des principales causes. Les reptiles sont particulièrement sensibles aux changements environnementaux, mais sont moins étudiés dans ce contexte. Mon étude vise à examiner l'effet paysager de l'agriculture sur l'abondance de la couleuvre rayée (*Thamnophis sirtalis*) et de la couleuvre à ventre rouge (*Storeria occipitomaculata*) en Ontario et au Québec, au Canada. Je m'attendais à ce que les couleuvres soient moins abondantes dans les sites avec plus d'agriculture dans le paysage environnant. Je m'attendais également à ce qu'elles soient en moyenne plus petites dans les zones plus agricoles. J'ai testé ces prédictions en estimant l'abondance des populations dans des zones humides intégrées dans un gradient de paysages agricoles et naturels autour d'Ottawa/Gatineau. Les sites ont été inventoriés une fois par semaine de mai à septembre en 2023 et 2024, et tous les serpents capturés ont été comptés, marqués et mesurés. Les couleuvres rayées et les couleuvres à ventre rouge capturées n'étaient pas moins abondantes dans les sites où la couverture agricole des terres environnantes était élevée, selon le modèle final; cependant, un modèle alternatif indiquait moins de serpents dans les zones humides avec plus d'agriculture environnante. La taille des couleuvres ne différait pas non plus significativement selon le gradient agricole.

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Introduction

The biodiversity loss crisis is one of the most pressing issues of the 21st century, with current extinction rates up to 100 - 1000 times higher than the background rate (Ceballos et al., 2015; IPBES, 2019; Pimm et al., 2014). Habitat destruction is the main cause of biodiversity loss in terrestrial ecosystems (IPBES, 2019; Newbold et al., 2015), with the conversion of natural landscapes to agriculture being one of the leading sources (Balouch et al., 2022; Cox et al., 2022; Newbold et al., 2015; Tan et al., 2023). Within the last decade, around two-thirds of global land has been altered for human use and as of 2019, agriculture occupied over one-third of the earth's land surface (FAOSTAT, 2021; IPCC, 2019).

Reptiles seem to be particularly sensitive to the impacts of land use change and habitat isolation (Keinath et al., 2017). One proposed reason for this is their lower dispersal capabilities compared to birds and mammals (Doherty et al., 2020; Guiller et al., 2022). While the hypothesis that decreased dispersal capacity leads to increased sensitivity to land use change was challenged by Martin et al. (2023), this did appear to be the case for reptiles, particularly regarding agriculture (Martin et al., 2023). Thus, reptiles may often be unable to escape a degrading habitat. While they are species-rich and proportionally one of the most threatened vertebrate taxa (Keinath et al., 2017), reptiles remain relatively understudied when it comes to the impacts of habitat loss and fragmentation (Doherty et al., 2020; Tan et al., 2023). Relative to birds and mammals, or even amphibians, we know comparatively little about reptile response to environmental change (Doherty et al., 2020; Tan et al., 2023).

The public's negative perception of reptiles has historically meant less concern for their conservation (Mullin and Siegel, 2011). However, reptiles not only provide a unique source of diversity, but can also serve as effective indicator species for ecosystem monitoring (Mullin and

Siegel, 2011). The life history traits that might make reptiles vulnerable to population decline and sensitive to environmental change (e.g., low reproductive rate, high site fidelity, high juvenile/neonate mortality, etc.) can make them useful for monitoring processes affecting the ecosystem (Mullin and Siegel, 2011). Therefore, reptiles are important taxa to conserve and warrant further study in habitat degradation and fragmentation research.

The current literature on reptile response to agriculture is mixed. Some studies suggest a negative impact of agriculture on reptiles (Doherty et al., 2020), seeing reduced species distribution (Guiller et al., 2022), declining abundance (Guiller et al., 2022; Reading & Jofré, 2015), lower species richness and diversity (Nopper et al., 2017; Ribeiro et al., 2009; Wasiolka & Blaum, 2011), altered community composition and lower species web connectivity (Kay et al., 2018), and reduced movement and dispersal through farmland (Row et al., 2012; Marshall et al., 2020). Not all species respond the same to anthropogenic land change, however, with some species being more abundant in grazed areas, for instance (Doherty et al., 2020). As such, other studies have found no effect of agriculture, for instance, seeing a positive effect of livestock removal on species richness, abundance, and composition in one habitat type but not another (Haby & Brandle, 2018), no effect of varying isolated habitat patches in agricultural lands on reptile species richness and abundance (Jellinek et al., 2014; Schutz & Driscoll, 2008), no significant differences in richness/diversity across successional stages in agricultural areas (Suazo-Ortuño et al., 2015), and that reptiles may willingly travel through farmland or even use it as habitat (albeit of potentially lower quality; Pulsford et al., 2018; Wisler et al., 2008).

There are several potential mechanisms behind why agriculture might negatively affect snakes. 1) Farmland could present an unfavourable habitat/matrix for snakes (Marshall et al., 2020; Row et al., 2012), resulting in smaller and/or isolated populations in smaller habitat

patches (MacArthur & Wilson, 2001). 2) Snakes may suffer direct mortality from agricultural machinery, as has been established in wood turtles (Tesauro et al., 2024). 3) Snakes could be adversely affected by pesticides (Hopkins et al., 2005). 4) People may intentionally harm snakes, given the generally negative perception of snakes. There are documented snake-human conflicts in several parts of the World (de Vera et al., 2024; Marshall et al., 2018; Whitaker & Shine, 2000).

Given the current literature, it appears the effect of agriculture on reptiles is not uniform and cannot necessarily be inferred from one species, region, or context to another. Species response likely depends on evolutionary history and life history traits, including habitat specialization (Keinath et al., 2017; Marshall et al., 2020; Tan et al., 2023). For instance, the movements of habitat specialists, like eastern fox snakes or king cobras, are impeded by agriculture (Row et al., 2012; Marshall et al., 2020). Thus, even if individuals are present in habitat patches within an agricultural matrix, they may become isolated within the patch and not have access to sufficient resources for a population to persist in the long term. More generalist species, however, may be more willing to traverse farmland and/or tolerate the altered landscape (Pulsford et al., 2018; Wisler et al., 2008). Pulsford et al. (2018) suggest this is a possibility because the species they observed in agricultural areas were generalists, while specialist species that were historically reported in the region were no longer found. The same species can respond differently in different parts of their range, with altered home range sizes, movement patterns, or habitat selection, for instance (Martino et al., 2012). As ectotherms, thermal quality is an important habitat feature for snakes and is a major driver in habitat selection, especially in colder climates (Diaz & Blouin-Demers, 2017; Harvey & Weatherhead, 2006; Row & Blouin-Demers, 2006). In contrast, in more climatically stable environments, where optimal temperatures are

easier to maintain, other factors, like prey availability or predator avoidance, might play a larger role. Thus, the response to changing landscapes may also differ in different regions. Most studies on reptile response to landscape modification take place in more southerly regions of the World (Doherty et al., 2020). Considering those that look specifically at snake response, the geographic scope is even more limited, with the majority of studies taking place in Australia, largely looking at the impacts of their predominant form of agriculture, grazing (Haby & Brandle, 2018; Jellinek et al., 2014; Kay et al., 2018; Pulsford et al., 2018; Reading & Jofré, 2015; Schutz & Driscoll, 2008). Agricultural practices differ across the globe, including the major types of agriculture (Connor, 2023), the level of mechanization and intensification (Daum, 2023; Waha et al., 2020), and pesticide use (Sharma et al., 2019). These differences could result in varying impacts on snake abundance in different regions.

I sought to quantify the impact of agriculture at the landscape scale on snake abundance to assess whether snakes can persist in habitat patches embedded in agricultural lands. I compared abundance in wetlands in Eastern Ontario and Southern Québec. My study area is close to the northernmost extent of snake distributions in North America. Thus, my research can help to fill knowledge gaps for northern snakes. A recent study by Gigeroff and Blouin-Demers (2023) studied landscape features in relation to garter snake and redbelly snake abundance in the same region, and while road density was the variable of interest, agriculture was also included. Agriculture was not a significant predictor of abundance in their findings; however, I wanted to extend on this work with sites selected specifically for variation in the amount of agriculture in the surrounding land. I also aimed to use natural habitat patches as the focal habitat rather than old fields (mostly of artificial origin) to examine agriculture through a landscape lens.

I estimated the abundance of garter snakes (*Thamnophis sirtalis*) and redbelly snakes (*Storeria occipitomaculata*) found in wetlands embedded in landscapes across a gradient from natural to agricultural. I expected higher abundance in wetlands surrounded by more natural habitats compared to agricultural land. I also expected snakes to be smaller on average in agricultural landscapes as a result of increased mortality and access to fewer resources preventing individuals from reaching larger sizes.

Methods

Study site and species

Garter snakes and redbelly snakes are both widely distributed and locally abundant in Ontario and Québec (Carpenter, 1952; Halliday & Blouin-Demers, 2018; Wright & Wright, 1994). Garter snakes are medium-sized generalist snakes found all over North America, occupying a range of habitat types (Carpenter, 1952). Redbelly snakes are smaller snakes and can also be found in a variety of habitats, mostly old fields, wet meadows, and edge habitat, including wetlands (Blanchard, 1937; Wright & Wright, 1994). I chose wetlands as field sites as they are an abundant habitat type in the area, including within farmland. While old fields tend to be the preferred habitat, wetlands are also used extensively by both snakes (Carpenter, 1952; Halliday & Blouin-Demers, 2018; Wright & Wright, 1994), and my goal was to have sites comprising natural habitat to examine agriculture on a landscape scale. I chose marshes as the focal habitat type for sites since they are more open and to keep habitat characteristics consistent at the local scale. I identified > 50 potential sites by inspecting a map of Ottawa/Gatineau in ArcGIS with the Ontario Land Cover Compilation v2.0 (OLCC) and Comptes des Terres du Québec (CTQ) layers to differentiate land cover types. I then selected sites after on-the-ground

visits, based on permission/accessibility and whether they were sufficiently open (not closed canopy) and had enough dry ground (not waterlogged or saturated) to place cover boards. This resulted in 31 wetlands in the Ottawa/Gatineau area (Figure 1) embedded in landscapes across a gradient of agricultural to natural. Each site was at least 1 km apart to maintain independence of site landscape composition and to prevent snake dispersal between sites.

Landscape variables

I quantified the land cover around each wetland within 100 m buffer increments, from 100 m – 1000 m (distances commonly used in studies of small vertebrates; Jackson & Fahrig, 2015). This was done to determine at what spatial scale the surrounding landscape composition had the greatest effect (i.e., the scale of maximum effect). Garter snakes and redbelly snakes typically travel well under 500 m (Blanchard, 1937; Carpenter, 1952), and have relatively small home ranges; up to 1000 m² for a similar species, Butler's garter snake (*Thamnophis butleri*; Shonfield et al., 2019), and potentially as small as 300 m² (Charland & Gregory, 1995). Thus, 1000 m was chosen as the maximum buffer size to encompass the area that snakes might move through in the summer. According to Jackson and Fahrig (2012), the scale of maximum effect tends to range from 0.3 – 0.5 times the maximum dispersal distance, and around 4 – 9 times the median dispersal distance. Given a maximum dispersal distance of under 400 m and an average dispersal distance of 130 m for a similar species (Eastern ribbonsnake, *Thamnophis sauritus*; Imlay et al., 2015), this range should be sufficient to capture the scale of maximum effect. Gigeroff and Blouin-Demers (2023) also found the scale of effect of most landscape variables for snake abundance for a similar study to fall within this range, suggesting this is an appropriate scale (Jackson & Fahrig, 2015).

Land cover types were initially classified using the OLCC and CTQ during site selection; however, to confirm land cover classification, I later used the Agriculture and Agri-Food Canada Annual Crop inventory 2021. I amalgamated land cover classes from 29 classes from OLCC, 9 from CTQ and 61 categories from the AAFC crop inventory into 5 categories: agriculture, forest, grassland/field, wetland, urban/developed, and open water (See Supplementary Information). I expected garter snakes and redbelly snakes to use forest, grassland/field, and wetland as habitat. Using the AAFC crop inventory layer, the land could be further categorized from “agriculture” into crop and pasture/forage. I analyzed the effect of crop and pasture post-hoc. I used road data from Statistics Canada 2024 Road Network to get road density (km road/km² area). Land cover types were verified using aerial imagery (City of Ottawa & National Capital Commission, 2017) and some ground-truthing.

Local site variables

I measured canopy/vegetation cover to capture local site variation that is likely to influence snake presence. Canopy and vegetation cover influence the amount of solar radiation the ground receives, affecting the thermal quality of the site, which is an important habitat variable for snakes (Blouin-Demers & Weatherhead, 2001, 2002; Harvey & Weatherhead, 2006; Row & Blouin-Demers, 2006). I measured vegetation cover at 10 randomly selected locations at each site, using ArcGIS to randomly generate point coordinates within 10 m of the transect (Supplementary Information; Figure SI 3: Sample wetland site viewed from ArcGIS Pro. The coordinates of cover boards along the sampling transects are depicted as black circles. I generated 10 random coordinates within a 10 m buffer along each transect to measure vegetation cover (pink circles). A total of 31 wetland sites (10 to 20 cover boards each) were surveyed from May to September 2023-24 across a gradient of agricultural landscapes.). I did this by placing a

camera at ground level and taking a picture facing upward to determine how much canopy and/or vegetation is in frame in a cone of 45° from the ground. This captures any vegetation that would sufficiently shade the location. I processed images in R, following a similar workflow set out by Houle et al. (2024) to binarize images to black and white. This converted blue/lighter pixels (open sky) to black and darker/non-blue pixels (vegetation cover) to white. The number of white pixels could then be summed to represent the proportion of vegetation cover relative to the amount of open sky. I validated these results against *cover2* (Chianucci et al., 2022), an R package that characterizes canopy cover attributes. This package gave very similar results most of the time, but was not as successful when pictures were taken in more overcast conditions with a darker sky. I organized images based on sky conditions and processed them accordingly.

Snake abundance

I used plywood cover boards (60 × 60 × 1.27 cm) to attract snakes by providing a warm hiding place (Halliday & Blouin-Demers, 2015). I placed boards along transects varying between 100 m and 200 m (depending on the size of the wetland), every 10 m. I estimated abundance by surveying each site every week from May to September, counting the number of snakes found under cover boards and those found incidentally along the transects between boards. Surveys were conducted between the hours of 08:00 and 18:00 on clear days when the air temperature was between 10 °C and 30 °C. I recorded the date, time, location, and air temperature for each survey. The vast majority of snakes (91% of garter, 99% of redbelly) were captured under the cover boards. I measured snakes from the tip of the snout to the end of the cloacal opening (snout-vent length; SVL), sexed them via probes, and uniquely marked each on the ventral scales anterior to the cloaca with a medical cautery unit, following Winne et al. (2006). I classified individuals that were too small to probe or accurately estimate the sex visually as “unsexed”. The

recapture rate was too low for accurate population size estimation with mark-recapture models (mean recapture rate of 8% for garter snakes and 7% for redbelly snakes), thus, the number of unique snakes captured was used as a proxy for abundance instead (Gigeroff & Blouin-Demers, 2023).

Statistical analyses

I modelled the relationship between agriculture, snake abundance, and snake size (SVL) in R (R Core Team, 2014), along with other land cover types and temporal variables that could influence snake abundance, like day of year, time of day, and temperature. To account for sampling effort, I assessed the number of snakes per survey, per site, for abundance models, and included an offset variable for the number of cover boards deployed at each site. I included a quadratic term for day of year since abundance is not expected to increase linearly throughout the season. I expect abundance to remain relatively stable or initially decline as individuals are lost from the population early in the field season and increase later in the summer when offspring are born. Likewise, for snake size, I expected a sudden decrease in size in the later half of the season as neonates are born and the likelihood of capturing smaller snakes increases. Inspection of pairwise correlation coefficients and variance inflation factors (VIFs) indicated that, for the abundance models, the quadratic day of year term was accounting for different variation in the data (Pearson's $r < 0.4$ and VIFs < 3) and was contributing greater explanatory power to the models (likelihood ratio tests, LRTs, were significantly better). However, for SVL models, the polynomial day of year terms showed extremely high pairwise correlation and collinearity (Pearson's $r > 0.9$ and VIFs > 150), indicating that both variables were explaining the same variation in the data for SVL. Because the quadratic day of year term was redundant and causing correlation and collinearity issues, I removed it from the SVL models. I constructed alternative

models with vegetation cover as a predictor variable, using just the 2024 observations since vegetation cover was not measured in 2023, and without vegetation cover, using the whole data set. Given a longer field season in 2024 and more sites, approximately three-quarters of snake observations were obtained in 2024. Thus, the dataset was not greatly reduced for models including vegetation cover. Abundance was modelled using generalized linear mixed models (GLMMs) with a negative binomial distribution, as is common for count data (and more flexible than Poisson; e.g. when variance > mean), and a log link function to ensure positive values, using lme4 and lmerTest (Bates et al., 2015; Kuznetsova et al., 2017). For SVL, I fit linear mixed-effects models (LMMs) using the package nlme (Pinheiro et al., 2025). I included a weighted variance structure for sex in the SVL models to deal with heteroskedasticity in residuals from unequal variance in sex. To account for individual variation across sites and pseudoreplication, since repeated observations were made at each site (multiple snake survey visits), I fit site as a random effect for all models. I fit year as a fixed effect because it falls below the suggested limit of > 5 levels for a random effect (Bolker et al., 2009; Oberpriller et al., 2022). I assessed model fit through diagnostic plots, including DHARMA plots (Hartig et al., 2024). I also plotted the raw data and residuals to get a sense of the distribution and trends.

To determine which land covers to include in the model, I plotted the percentage of each land cover across sites to determine whether sites varied appreciably for each land cover (see Supplementary Information: Figure SI 4: Variation in the proportion of the different land covers by site, for 31 wetland sites, using agriculture as the land cover of interest (A), and land cover proportions using crop and pasture as the land covers of interest (B). Sites were selected across a gradient of agricultural landscapes in Ottawa/Gatineau and surveyed from May to September 2023-24.). The percentage of open water, grassland, and road density in the landscape showed

very little variation across sites (Supplementary Information: Figure SI 4), and so to avoid over-parameterization, they were not included in the model. This resulted in the inclusion of agriculture, forest, urban, and wetland cover. In a separate model, I used crop, pasture, forest, urban, and wetland covers to look at the effect of crop and pasture/forage post-hoc, compared to the broader classification of “agriculture”. Because I selected sites based on the layer that categorized the land by agriculture, however, there was not as much variation across sites for the percentage of crop cover (0% to 51%) or pasture/forage (0% to 55%), being highly skewed to lower percentages (Supplementary Information).

The scale of maximum effect for each land cover was determined by taking the Pearson’s correlation coefficient between abundance and the land covers at each buffer size, and likewise for SVL (Table 1 and Table 2). To check for correlation and collinearity among all variables, I assessed the correlation matrices for each model’s set of variables and calculated VIFs (Supplementary Information: Table SI 1) from the car package in R (Fox & Weisberg, 2019). If variables were strongly correlated, one was removed from the model.

I centred and scaled variables for the abundance models, and non-significant control variables were removed to simplify the models and help with convergence. Data exploration plots for abundance and SVL data against each predictor variable showed little to no trend for the control variables that were removed (see Supplementary Information: Figure SI 7 - Figure SI 10). Reduced models were compared via LRT, corrected Akaike's Information Criterion (AICc), and coefficient of determination (R^2) to confirm that dropping non-significant terms did not affect model performance. I shifted survey times on very hot days and days with cooler mornings so that surveys were conducted during more optimal temperatures, which likely explains why temperature was not a significant predictor in most of the models and could be removed. Time of

day and temperature are also likely somewhat redundant as controls since both account for thermal conditions of the site. I also used LRTs for null hypothesis testing to compare the explanatory power of percent agriculture in the models.

Results

Snake abundance

Across all sites, I captured 254 individual garter snakes (286 total captures) and 134 individual redbelly snakes (158 total captures). Of the captured snakes, 236 garter snakes (93%) and 133 redbelly snakes (99%) were under cover boards. The sex ratio was relatively even for garter snakes (36% female, 30% male, and 33% unsexed), but was skewed towards unsexed for redbelly snakes (27% females, 19% males, 54% unsexed) due to the difficulty of sexing small snakes. Garter snakes ranged in size from 13 cm to 70 cm SVL, while redbelly snakes ranged in size from 6 cm to 29 cm SVL.

Predictors of garter snake abundance

The scale of maximum effect ranged from 400 m to 1000 m for garter snake abundance (Table 1). Having the scale of maximum effect at the boundary of the buffer size range typically suggests the need for larger buffer sizes; however, the correlation coefficient did not vary greatly across buffer sizes for each land cover (Supplementary Information), and given the small typical distances snakes travel (Blanchard, 1937; Carpenter, 1952; Charland & Gregory, 1995), a 1000 m buffer size is likely sufficient.

The final model for garter snake abundance included percent agriculture, wetland, and urban land covers, day of year², time of day, and vegetation cover as predictors. Significant

predictors of garter snake abundance under the final model were day of year², time of day, vegetation cover, and percent urban cover. More snakes were found at sites with lower vegetation cover and found later in the day. Snake abundance slightly declined throughout the season and then increased later in the summer. Fewer snakes were found at sites with more urban land cover in the surrounding landscape (Table 3). There was no significant difference in the abundance of garter snakes in wetlands with increasing agriculture in the surrounding landscape, though it was nearly significant, with the model predicting 9% fewer garter snakes per 10% increase in agriculture (95% CI [-19, 3], $p = 0.13$; Figure 2: Model-predicted garter snake abundance (A) and redbelly snake abundance (B) versus the percentage of agricultural land cover in the landscape. Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24. Trend lines were predicted from the final selected models including vegetation cover as a predictor.)

For the alternative model using the full data set (both years) without vegetation cover, agriculture was a significant predictor of garter snake abundance, indicating 17% fewer snakes per 10% increase in agricultural cover in the landscape, (95% CI [-30, -2], $p = 0.03$; Supplementary Information: Figure SI 11: Model-predicted garter snake abundance (A) and redbelly abundance (B) versus the percentage of agricultural land cover in the landscape. Trend lines were predicted from the alternative models without vegetation cover, using the full dataset for both years. Snake abundance was surveyed at 31 wetland sites across an agricultural gradient in Ottawa/Gatineau from May to September 2023-24.).

For the model looking at crop and pasture, garter snake abundance did not differ significantly with increasing crop or pasture cover in the surrounding landscape. The model predicted 9% fewer snakes per 10% increase in crop cover in the landscape

(95% CI [-22, 6], $p = 0.22$) and 3% fewer snakes per 10% increase in pasture cover (95% CI [-17, 14], $p = 0.71$; Supplementary Information: Figure SI 15: Model-predicted garter snake abundance (A) and redbelly abundance (B) versus the percentage of agricultural land cover in the landscape. Trend lines were predicted from the models looking at crop and pasture separately, instead of “agriculture” more broadly. Snake abundance was surveyed at 31 wetland sites across an agricultural gradient in Ottawa/Gatineau from May to September 2023-24.), however, these effects were not significant.

Predictors of redbelly snake abundance

The scale of maximum effect for redbelly snake abundance ranged from 100 m to 1000 m (Table 1). The final model included percent agriculture, wetland, and urban land covers, day of year², time of day, and vegetation cover. Only time of day was significant, with more snakes being found later in the day (Table 3). There was no significant difference in the abundance of redbelly snakes in wetlands with increasing agricultural land in the surrounding landscape, though the model predicted 11% fewer redbelly snakes per 10% increase in agricultural land cover (95% CI [-38, 27], $p = 0.52$; Figure 2).

The results for the alternative full data set model without vegetation cover were similar to the selected model for redbelly snake abundance; agriculture was still not a significant predictor and similarly predicted 12% fewer snakes per 10% increase in agricultural cover in the landscape (95% CI [-36, 22], $p = 0.44$; Supplementary Information: Figure SI 11).

Examining crop and pasture, there was no significant difference in redbelly snake abundance with increasing crop cover in the landscape, though the model predicted 33% fewer

redbelly snakes per 10% increase in crop cover (95% CI [-67, 39], $p = 0.28$). For percent pasture, the model predicted 8% fewer snakes with a 10% increase in pasture cover (95% CI [-47, 61], $p = 0.78$; Supplementary Information: Figure SI 15). These effects were not significant, however.

Predictors of garter snake size

The scale of maximum effect for garter snake size ranged from 200 m to 1000 m (Table 2: Pearson's correlation coefficients for the buffer sizes of the percentages of different land covers around wetland sites corresponding to the scale of maximum effect for garter snake and redbelly snake size (snout-vent-length; SVL). Land covers were classified in ArcGIS Pro using the Ontario Land Cover Compilation, Comptes des Terres de Québec, and the Agriculture and Agri-Food Annual Crop Inventory. Snake abundance was surveyed at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24.). The final model for garter snake size included percent agriculture, wetland, and urban land covers, sex, day of year, time of day, and vegetation cover as predictors. Sex, day of year, and wetland were significant predictors, expecting male or unsexed snakes to be smaller than females, and expecting to see more small snakes later in the summer. Garter snakes tended to be slightly larger at sites with more wetland cover in the surrounding landscape, with the model predicting 0.6 cm larger snakes per 10% increase in wetlands in the landscape (95% CI [0.03, 1.15], $p = 0.04$). Garter snakes did not differ significantly in size across sites with increasing agricultural land cover in the landscape, though the model predicted 0.3 cm smaller snakes per 10% increase in agriculture in the landscape (95% CI [-0.77, 0.18], $p = 0.21$; Figure 3). Agricultural land cover would need to increase 33% to see a 1 cm difference in garter snake size.

The results of the model without vegetation cover were similar to the selected model, expecting 0.1 cm smaller snakes per 10% increase in agriculture in the landscape (95% CI [-0.59, 0.33], $p = 0.57$; Supplementary Information: Figure SI 12). Agricultural land cover would need to increase 78% to see a 1 cm difference in snake size.

Looking at the effect of crop and pasture, snake size did not differ significantly with increasing crop or pasture cover in the landscape either, with the model predicting smaller snakes by 0.4 cm per 10% crop cover increase (95% CI [-1.21, 0.41], $p = 0.31$) and 0.3 cm per 10% pasture cover increase (95% CI [-0.89, 0.32], $p = 0.34$; Supplementary Information: Figure SI 16). A 25% increase in crop cover, or 35% increase in pasture cover, would be required to see a 1 cm difference in snake size.

To assess whether the inclusion of unsexed individuals was affecting the size differences; for example, if there were more juveniles and larger snakes at sites with less agriculture in the landscape, models were re-fit, excluding unsexed individuals from the dataset. However, this resulted in similar effect sizes and significance for percent agriculture, percent crop, and percent pasture parameters (see Table 7).

Predictors of redbelly snake size

The scale of maximum effect for redbelly snake size ranged from 100 m to 1000 m (Table 4). The final model for redbelly snake SVL included percent agriculture, wetland, forest, and urban land covers, day of year, time of day, sex, and vegetation cover as predictors. Sex and temperature were the only significant predictors of redbelly snake size, with male or unsexed snakes being smaller than females, and finding more snakes at warmer temperatures. Redbelly

snake size did not differ significantly with increasing agricultural land cover in the landscape, with the model predicting 0.2 cm smaller snakes per 10% increase in agriculture by the model (95% CI [-0.7, 0.2], $p = 0.29$; Figure 3). Agricultural land cover would need to increase 41% to see a 1 cm difference in redbelly snake size. Percent agriculture and percent wetland were partially correlated ($r = 0.5$), but this was below the generally cited threshold of 0.7 for concern about multicollinearity (Fisher & Yates, 1990).

For the full data set model without vegetation cover, agriculture was again not a significant predictor of snake size and also had a very small effect, predicting 0.06 cm larger per 10% agricultural increase (95% CI [-0.4, 0.5], $p = 0.77$; Supplementary Information: Figure SI 12). Agricultural land cover would need to increase 172% to see a 1 cm difference in redbelly snake size, according to the model. Percent agriculture and percent wetland were partially correlated ($r = 0.54$).

For the model looking at crop and pasture, redbelly snake size did not differ significantly with increasing crop or pasture cover in the landscape, though the models predicted 0.4 cm larger snakes per 10% crop cover increase (95% CI [-0.3, 1], $p = 0.26$). A 27% increase in crop cover would be required to see a 1 cm difference in snake size. For pasture cover, the model predicted 0.6 cm smaller snakes per 10% pasture cover increase (95% CI [-1.5, 0.3], $p = 0.22$; Supplementary Information: Figure SI 16), requiring a 16% increase in crop cover to see a 1 cm difference in snake size. To assess whether the inclusion of unsexed individuals affected size differences, I re-fit the models excluding unsexed individuals from the dataset, but this resulted in similar effect sizes and significance (Table 8).

Discussion

Landscape effect of agriculture on garter and redbelly snakes

In examining the effect of agriculture in the surrounding landscape on garter and redbelly snake abundance in wetlands, my results suggest that snake population size may decline with increasing surrounding agricultural land cover. The number of garter snakes and redbelly snakes could decrease nearly linearly with increasing amounts of agriculture in the surrounding landscape. While these results were not significant, under the alternative models, which used the full data set for both years but did not include vegetation cover as a predictor, the effect of agriculture was significant for garter snake abundance and nearly significant for redbelly snake abundance. Thus, the negative effect of agriculture in the surrounding landscape seems to be influenced by local-scale variation and is likely more complex than just how much is present in the surrounding area and may be influenced by other factors.

In terms of SVL, garter and redbelly snake size did not differ across the agricultural gradient. Even if the effects were significant, the effect size for expected size differences with increasing amounts of agriculture in the landscape were not biologically significant, requiring a minimum of a 33% increase in agricultural cover, or a 16% increase in crop cover, to see a single centimetre difference in snake size. This opposes my prior expectations of seeing smaller snakes on average in wetlands with a higher percentage of surrounding agricultural land. This suggests that higher amounts of agriculture in the landscape may not greatly restrict access to resources or cause higher mortality such that individuals are unable to reach larger sizes. This did not appear to be an artifact of the possibility of there being more juvenile snakes in sites with lower agricultural cover skewing size differences.

Finding no significant results for the amount of agricultural cover in the landscape on snake abundance or size falls in agreement with studies finding neutral/nonsignificant effects of agriculture on reptile abundance/presence (Jellinek et al., 2014; Pulsford et al., 2018; Schutz & Driscoll, 2008; Suazo-Ortuño et al., 2015). However, Pulsford et al. (2018) looked at the response of frogs and lizards, which likely differ in habitat needs and dispersal from snakes. Furthermore, Pulsford et al. (2018) and Suazo-Ortuño et al. (2015) looked specifically at the effects of grazing on a local scale, while I looked at a mix of cropping and grazing agriculture, and at the landscape scale. The scale at which the effects of agriculture are being examined is important; my results differed when some measure of local scale variation (i.e. vegetation cover) was included in the model or not. Without vegetation cover in the model, agriculture was a significant negative predictor, however, when it was included in the model, the effect of agriculture was reduced in effect size and significance. This is similar to the findings of Haby et al. (2018), who only found a difference in reptile abundance across grazed and ungrazed sites at the microhabitat scale and no difference at the macrohabitat scale, supporting the importance of scale and local characteristics. The effect of agriculture may be stronger at a local scale (Guiller et al., 2022; Reading & Jofré, 2015; Wasiolka & Blaum, 2011 found negative effects at local scales), where habitat tends to be directly replaced, compared to in the surrounding landscape, where natural habitat can remain. However, other studies have found a negative effect of agriculture at larger scales as well (Ribeiro et al., 2009; Row et al., 2012), and while my results were not significant, the effect sizes fall more in agreement with these findings.

Agriculture and habitat heterogeneity

The results of this study suggest that wetlands in agricultural landscapes may still support snake populations, however, they could be reduced in size and may no longer sufficiently

support populations if the surrounding landscape becomes too agriculturally dominant. Given the lack of significance of my results, other factors likely influence the strength of this effect. In general, habitat heterogeneity likely benefits snakes (Wisler et al., 2008). Being able to access different land cover types can provide different resources or functions, like using open habitats for basking and using others to retreat to or access different resources. Snakes in temperate regions tend to prefer edge habitat (Blouin-Demers & Weatherhead, 2001, 2002; DeGregorio, 2011; Wisler et al., 2008), and Wisler et al. (2008) suggest that agriculture, while not primary habitat, may be used by snakes to thermoregulate. Habitat preference can change across scales as well; Row et al. (2012) found a preference for wetlands at large scales and a preference for dry open areas at smaller local scales. Row and colleagues further suggest that fragmentation might be neutral or beneficial to reptiles in temperate regions (Row et al., 2012), as it can provide access to thermally superior edge habitat while maintaining access to other habitats within the landscape. The degree of heterogeneity may also make a difference, with finer-grained landscapes (i.e. greater changes in landscape at smaller distances) likely supporting reptiles more than coarse-grained ones (Pulsford et al., 2018). Thus, snakes may be more likely to persist in more heterogeneous agricultural landscapes with natural land cover present, but less likely to in homogeneous agricultural landscapes. This is likely also influenced by factors like the type of agriculture or the kind of land management.

Limitations and future directions

A stronger effect of agriculture on a landscape scale may have been found with a larger sample size or with sites surrounded by higher proportions of agriculture. The highest percentage of agricultural land cover was around 80% in this study, which still maintains some potential access to other land cover types. If I had sites surrounded entirely by agriculture, there may have

been more of an effect. Given that the scale of maximum effect for several land cover variables fell on the largest buffer size, and the fact that recapture rates were very low, the true scale of maximum effect could have fallen beyond this range and therefore could affect the significance of the results. However, given that the correlation coefficient varied very little over the range of buffer sizes (Figure SI 5 and Figure SI 6), the effect may not have been very different. Percent forest was correlated with percent agriculture and percent crop for several models; therefore, the effect of agriculture cannot be fully disentangled from the concurrent effect of decreasing forest in the landscape.

There could also be variation in the effect that agriculture has on a landscape scale depending on other spatial characteristics as well, such as differing sizes of wetland patches or their configuration and connectivity to other natural habitat patches. The percentage of agriculture in the landscape indirectly compares the degree of isolation of a wetland patch, as a more isolated site will have less natural land cover surrounding it, however, the proximity to other natural land cover could affect how easily snakes are able to access it. While some studies found no effect of patch configuration or connectivity (Jellinek et al., 2014; Schutz & Driscoll, 2008), this could be taxon-dependent. Other studies have found that snakes generally avoid using or travelling through agriculture (Marshall et al., 2020; Row et al., 2012), which suggests that lower connectivity could have an effect.

The type of agriculture also likely plays a large role in determining the impact that agriculture has, and so studying its effects could benefit from a more nuanced approach. It is not uncommon to look at agriculture in a broad sense (Guiller et al., 2022; Jellinek et al., 2014; Kay et al., 2018; Schutz & Driscoll, 2008; Suazo-Ortuño et al., 2015), however, the effect of different kinds of agriculture, such as grazing versus cropping, likely differs, and so the overall effect

could be nullified. Grazing likely has a more neutral effect on snakes (Doherty et al., 2020), given that there are typically fewer agrochemical inputs, pastures are more likely to have natural vegetation and/or resemble old field habitat more closely, and have less machinery and harvesting disturbance. My post-hoc examination of crop and pasture predicted greater population declines with increasing surrounding crop cover versus pasture cover for snake abundance (though still non-significant). Unexpectedly, pasture cover had a negative effect on redbelly snake size while crop cover had a positive effect (though not significant and extremely small effect size). I had modest variation across sites for percent crop and percent pasture, giving weak explanatory power to the results. Furthermore, even with the land cover layer that differentiated the types of agricultural lands, pasture and forage were classified in a single category; while this grouping makes sense on a functional-use viewpoint, they may differ in snake suitability. Pasture is likely more hospitable for snakes since there is no mechanical harvesting of the land compared to growing forage, like hay.

Implications of increasing agriculture

Potential implications of this research include assessing whether wetland habitat patches in agricultural landscapes can support snake populations. This is impacted by land management and decisions on land clearing, such as leaving areas of natural land cover within agricultural landscapes rather than clearing entire areas. Such topics have been debated in ecology, including the biodiversity value of several small versus single large habitat patches debate. It may be possible to offset the negative effects of agriculture on snakes as long as there are other land covers and habitat around for individuals to move between. The availability and quality of microhabitats around/within agricultural land could also impact the effects of agriculture. Practices such as planting hedgerows or maintaining a natural vegetation buffer around fields,

using cover crops or fallow fields in plot rotations, using fewer pesticides, etc., could all affect this. Future research should be done to disentangle the mechanisms behind agriculture that negatively affect snakes.

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Tables

Table 1: Pearson's correlation coefficients for the buffer sizes of the percentages of different land covers around wetland sites corresponding to the scale of maximum effect for garter snake and redbelly snake abundance. Land covers were classified in ArcGIS Pro using the Ontario Land Cover Compilation, Comptes des Terres de Québec, and the Agriculture and Agri-Food Annual Crop Inventory. Snake abundance was surveyed at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24.

| Land cover | Predictor variable | Pearson's correlation coefficient |
|---------------------|--------------------------|-----------------------------------|
| Agriculture (400m) | Garter snake abundance | -0.2 |
| Crop (1000m) | Garter snake abundance | -0.1 |
| Pasture (900m) | Garter snake abundance | -0.2 |
| Forest (800m) | Garter snake abundance | 0.07 |
| Wetland (1000m) | Garter snake abundance | 0.3 |
| Urban (700m) | Garter snake abundance | -0.1 |
| Agriculture (1000m) | Redbelly snake abundance | -0.1 |
| Crop (300m) | Redbelly snake abundance | -0.1 |
| Pasture (900m) | Redbelly snake abundance | -0.07 |
| Forest (100m) | Redbelly snake abundance | -0.1 |
| Wetland (1000m) | Redbelly snake abundance | 0.2 |
| Urban (100m) | Redbelly snake abundance | -0.1 |

Table 2: Pearson’s correlation coefficients for the buffer sizes of the percentages of different land covers around wetland sites corresponding to the scale of maximum effect for garter snake and redbelly snake size (snout-vent-length; SVL). Land covers were classified in ArcGIS Pro using the Ontario Land Cover Compilation, Comptes des Terres de Québec, and the Agriculture and Agri-Food Annual Crop Inventory. Snake abundance was surveyed at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24.

| Land cover | Predictor variable | Pearson’s correlation coefficient |
|---------------------|---------------------------|--|
| Agriculture (1000m) | Garter snake SVL | -0.07 |
| Crop (800m) | Garter snake SVL | 0.07 |
| Pasture (900m) | Garter snake SVL | -0.2 |
| Forest (200m) | Garter snake SVL | -0.2 |
| Wetland (300m) | Garter snake SVL | 0.2 |
| Urban (1000m) | Garter snake SVL | -0.1 |
| Agriculture (100m) | Redbelly snake SVL | -0.09 |
| Crop (800m) | Redbelly snake SVL | 0.08 |
| Pasture (800m) | Redbelly snake SVL | -0.2 |
| Forest (600m) | Redbelly snake SVL | -0.1 |
| Wetland (1000m) | Redbelly snake SVL | 0.1 |
| Urban (300m) | Redbelly snake SVL | -0.2 |

Table 3: Summary statistics for the final selected generalized linear mixed models for garter snake and redbelly snake abundance. Snake abundance was surveyed at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24. Parameter estimates are on a log scale and were centred and scaled.

| Model: Garter snake abundance | | | | | |
|--|----------|----------------|---------|---------|-----|
| Parameter | Estimate | Standard error | z value | p-value | |
| (Intercept) | -3.59 | 0.15 | -23.52 | < 0.00 | *** |
| Agriculture (400m) | -0.19 | 0.13 | -1.51 | 0.13 | |
| Wetland (1000m) | 0.13 | 0.11 | 1.21 | 0.22 | |
| Urban (700m) | -0.34 | 0.12 | -2.77 | 0.01 | ** |
| Day of year | -0.17 | 0.10 | -1.66 | 0.10 | . |
| Day of year ² | -0.29 | 0.11 | -2.75 | 0.01 | ** |
| Time of day | 0.46 | 0.10 | 4.68 | < 0.00 | *** |
| Vegetation cover | -0.30 | 0.11 | -2.85 | < 0.00 | ** |
| Model: Redbelly snake abundance | | | | | |
| Parameter | Estimate | Standard error | z value | p-value | |
| (Intercept) | -5.62 | 0.48 | -11.78 | 0.00 | *** |
| Agriculture (1000m) | -0.28 | 0.43 | -0.64 | 0.52 | |
| Wetland (1000m) | 0.54 | 0.40 | 1.37 | 0.17 | |
| Urban (100m) | 0.08 | 0.35 | 0.24 | 0.81 | |
| Day of year | -0.21 | 0.13 | -1.58 | 0.11 | |
| Day of year ² | 0.15 | 0.14 | 1.07 | 0.28 | |
| Time of day | 0.49 | 0.13 | 3.66 | 0.00 | *** |
| Vegetation cover | 0.20 | 0.24 | 0.82 | 0.41 | |

Table 4: Summary statistics for the final selected linear mixed models for garter snake and redbelly snake size (snout-vent-length; SVL). Snakes were sampled at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24.

| Model: Garter snake SVL | | | | | | |
|----------------------------------|----------|----------------|-----|---------|---------|-----|
| Parameter | Estimate | Standard error | DF | t-value | p-value | |
| (Intercept) | 50.64 | 3.53 | 156 | 14.35 | < 0.00 | *** |
| Agriculture (1000m) | -0.03 | 0.02 | 24 | -1.29 | 0.21 | |
| Wetland (300m) | 0.06 | 0.03 | 24 | 2.16 | 0.04 | * |
| Urban (1000m) | -0.05 | 0.07 | 24 | -0.75 | 0.46 | |
| Day of year | -0.04 | 0.01 | 156 | -3.34 | < 0.00 | ** |
| Time of day | 0.22 | 0.20 | 156 | 1.09 | 0.28 | |
| Sex (unsexed) | -7.98 | 1.74 | 156 | -4.59 | < 0.00 | *** |
| Sex (male) | -26.02 | 1.43 | 156 | -18.26 | < 0.00 | *** |
| Vegetation cover | -0.76 | 2.28 | 156 | -0.33 | 0.74 | |
| Model: Redbelly snake SVL | | | | | | |
| Parameter | Estimate | Standard error | DF | t-value | p-value | |
| (Intercept) | 22.64 | 2.30 | 81 | 9.84 | 0.00 | *** |
| Agriculture (100m) | -0.02 | 0.02 | 11 | -1.11 | 0.29 | |
| Forest (600m) | -0.01 | 0.01 | 11 | -1.01 | 0.34 | |
| Wetland (1000m) | 0.02 | 0.02 | 11 | 0.81 | 0.44 | |
| Urban (300m) | 0.02 | 0.04 | 11 | 0.60 | 0.56 | |
| Day of year | -0.01 | 0.01 | 81 | -1.42 | 0.16 | |
| Temperature (C) | 0.12 | 0.05 | 81 | 2.31 | 0.02 | * |
| Sex (unsexed) | -1.71 | 0.57 | 81 | -3.03 | < 0.00 | ** |
| Sex (Male) | -9.02 | 0.74 | 81 | -12.16 | < 0.00 | *** |
| Vegetation cover | 1.39 | 1.41 | 81 | 0.99 | 0.32 | |

Table 5: Model comparison results for the likelihood ratio test (LRT) and corrected Akaike Information Criterion (AICc) comparing reduced models to the full models for garter snake and redbelly snake abundance. Snake abundance was surveyed at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24.

| Models: Garter snake abundance | | | | | | | | |
|---|--------|--------|--------|----------------|----------|--------|----|---------|
| Models | AIC | AICc | BIC | Log Likelihood | Deviance | Chi sq | DF | p-value |
| Reduced model | 663.59 | 664.08 | 704.88 | -321.80 | 643.59 | | | |
| Full model | 665.40 | 666.1 | 714.95 | -320.70 | 641.40 | 2.19 | 2 | 0.33 |
| Models: Redbelly snake abundance | | | | | | | | |
| Models | AIC | AICc | BIC | Log Likelihood | Deviance | Chi sq | DF | p-value |
| Reduced model | 406.65 | 407.14 | 447.94 | -193.33 | 386.65 | | | |
| Full model | 406.22 | 406.92 | 455.77 | -191.11 | 382.22 | 4.431 | 2 | 0.11 |

Table 6: Model comparison results for the likelihood ratio test (LRT) and corrected Akaike Information Criterion (AICc) comparing reduced models to the full models for garter snake and redbelly snake snout-vent-length (SVL). Snakes were sampled at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24.

| Models: Garter snake SVL | | | | | | |
|-----------------------------------|---------|---------|---------|----------------|----|---------|
| Models | AIC | AICc | BIC | Log Likelihood | DF | p-value |
| Reduced model | 1318.56 | 1320.64 | 1360.70 | -646.28 | 13 | |
| Full model | 1322.35 | 1325.12 | 1370.98 | -646.17 | 15 | 0.90 |
| Models: Redbelly snake SVL | | | | | | |
| Models | AIC | AICc | BIC | Log Likelihood | DF | p-value |
| Reduced model | 505.68 | 512.29 | 542.43 | -238.84 | 14 | |
| Full model | 506.71 | 510.51 | 546.08 | -238.35 | 15 | 0.32 |

Table 7: Parameter estimates for interest variables, percent agriculture or percent crop and percent pasture, for garter snake size (snout-vent-length; SVL) models when unsexed individuals (too small to sex; primarily juveniles) are included and excluded from the dataset. Snakes were sampled at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24.

| Model: Garter snake SVL | | | | | | |
|--|---------------------|----------|----------------|----|---------|---------|
| Condition | Parameter | Estimate | Standard error | DF | t-value | p-value |
| With unsexed | Agriculture (1000m) | -0.03 | 0.02 | 24 | -1.29 | 0.21 |
| Without unsexed | Agriculture (1000m) | -0.01 | 0.06 | 21 | -0.24 | 0.81 |
| Model: Garter snake SVL (no vegetation cover) | | | | | | |
| Condition | Parameter | Estimate | Standard error | DF | t-value | p-value |
| With unsexed | Agriculture (1000m) | -0.01 | 0.02 | 24 | -0.57 | 0.57 |
| Without unsexed | Agriculture (1000m) | -0.02 | 0.05 | 22 | -0.41 | 0.69 |
| Model: Garter snake SVL (crop and pasture) | | | | | | |
| Condition | Parameter | Estimate | Standard error | DF | t-value | p-value |
| With unsexed | Crop (800m) | -0.04 | 0.04 | 23 | -1.03 | 0.31 |
| Without unsexed | Crop (800m) | 0.07 | 0.08 | 20 | 0.84 | 0.41 |
| With unsexed | Pasture (900m) | -0.03 | 0.03 | 23 | -0.97 | 0.34 |
| Without unsexed | Pasture (900m) | -0.10 | 0.09 | 20 | -1.10 | 0.28 |

Table 8: Parameter estimates for interest variables, percent agriculture or percent crop and percent pasture, for redbelly snake size (snout-vent-length; SVL) models when unsexed individuals (too small to sex; primarily juveniles) are included and excluded from the dataset. Snakes were sampled at 31 wetland sites across Ottawa/Gatineau. Snake abundance was surveyed from May to September 2023-24 over an agricultural gradient.

| Model: Redbelly snake SVL | | | | | | |
|--|--------------------|----------|----------------|----|---------|---------|
| Condition | Parameter | Estimate | Standard error | DF | t-value | p-value |
| With unsexed | Agriculture (100m) | -0.02 | 0.02 | 11 | -1.11 | 0.29 |
| Without unsexed | Agriculture (100m) | -0.02 | 0.03 | 10 | -0.85 | 0.42 |
| Model: Redbelly snake SVL (no vegetation cover) | | | | | | |
| Condition | Parameter | Estimate | Standard error | DF | t-value | p-value |
| With unsexed | Agriculture (100m) | 0.01 | 0.02 | 12 | 0.30 | 0.77 |
| Without unsexed | Agriculture (100m) | -0.01 | 0.02 | 11 | -0.52 | 0.62 |
| Model: Redbelly snake SVL (crop and pasture) | | | | | | |
| Condition | Parameter | Estimate | Standard error | DF | t-value | p-value |
| With unsexed | Crop (800m) | 0.04 | 0.03 | 11 | 1.20 | 0.26 |
| Without unsexed | Crop (800m) | 0.04 | 0.02 | 10 | 1.68 | 0.12 |
| With unsexed | Pasture (800m) | -0.06 | 0.04 | 11 | -1.49 | 0.16 |
| Without unsexed | Pasture (800m) | -0.06 | 0.03 | 10 | -1.87 | 0.09 |

Figures

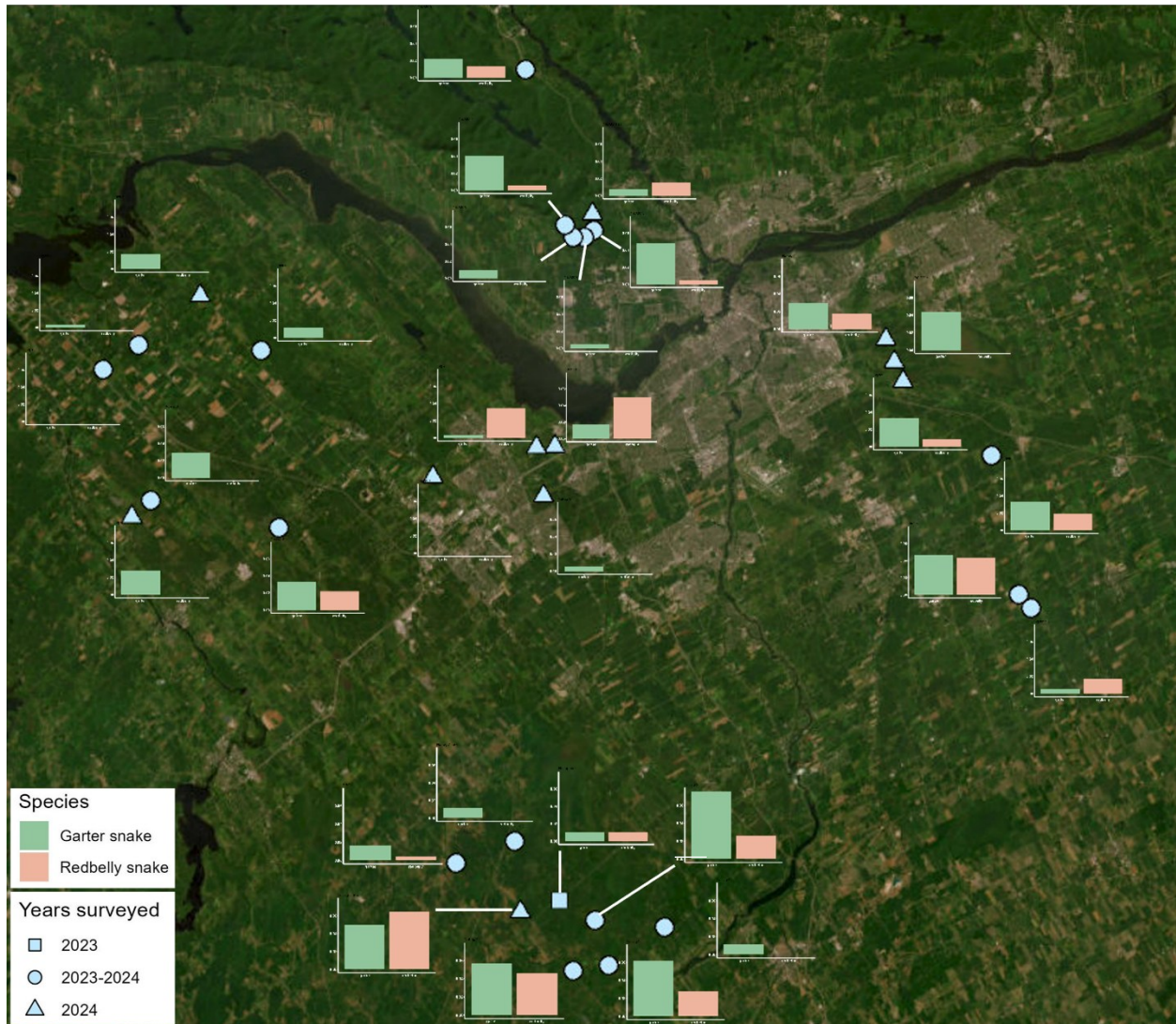


Figure 1: Standardized garter snake and redbelly snake abundance (snakes per cover board, per survey) for each field site. Square points represent sites that were visited only in 2023, triangles represent sites that were only visited in 2024, and circles represent sites that were visited both years. A total of 31 sites were surveyed across a gradient of agricultural landscapes in Ottawa/Gatineau, from May to September. Green bars represent garter snake abundance and red/orange bars represent redbelly snake abundance.

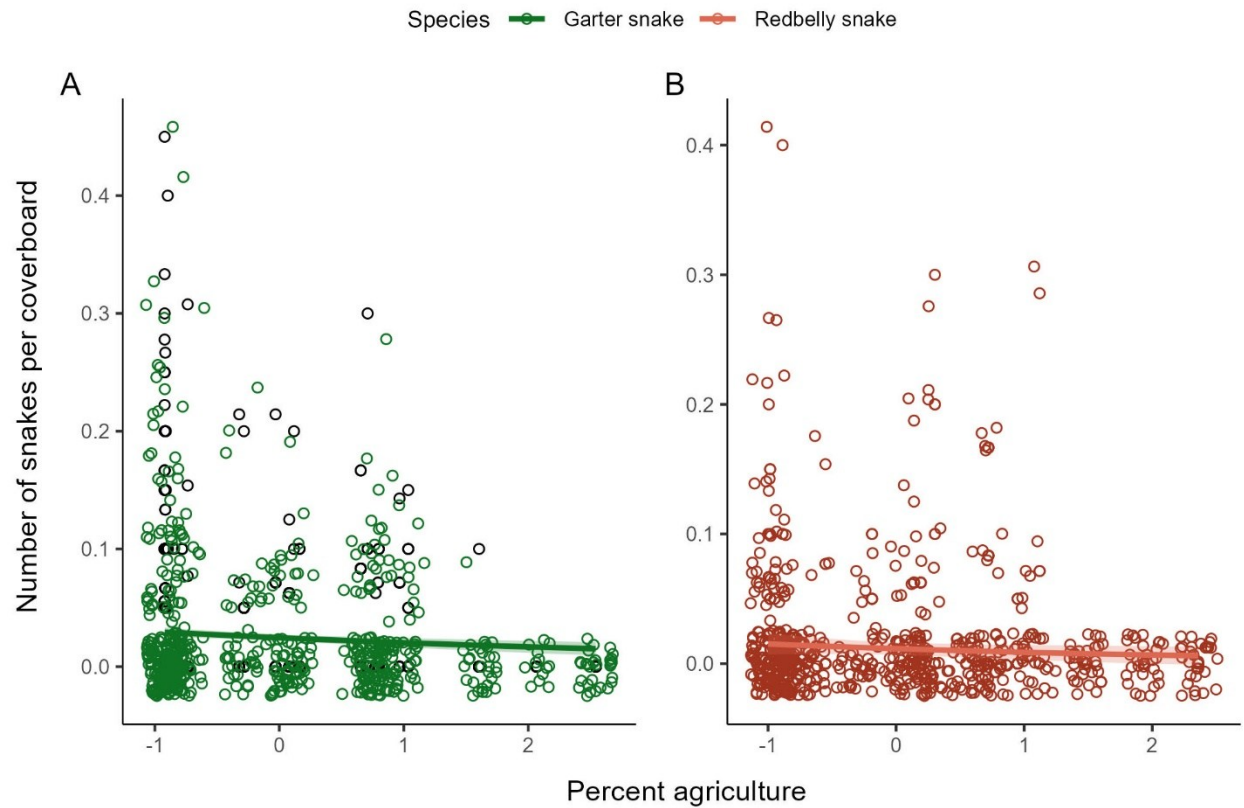


Figure 2: Model-predicted garter snake abundance (A) and redbelly snake abundance (B) versus the percentage of agricultural land cover in the landscape. Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24. Trend lines were predicted from the final selected models including vegetation cover as a predictor.

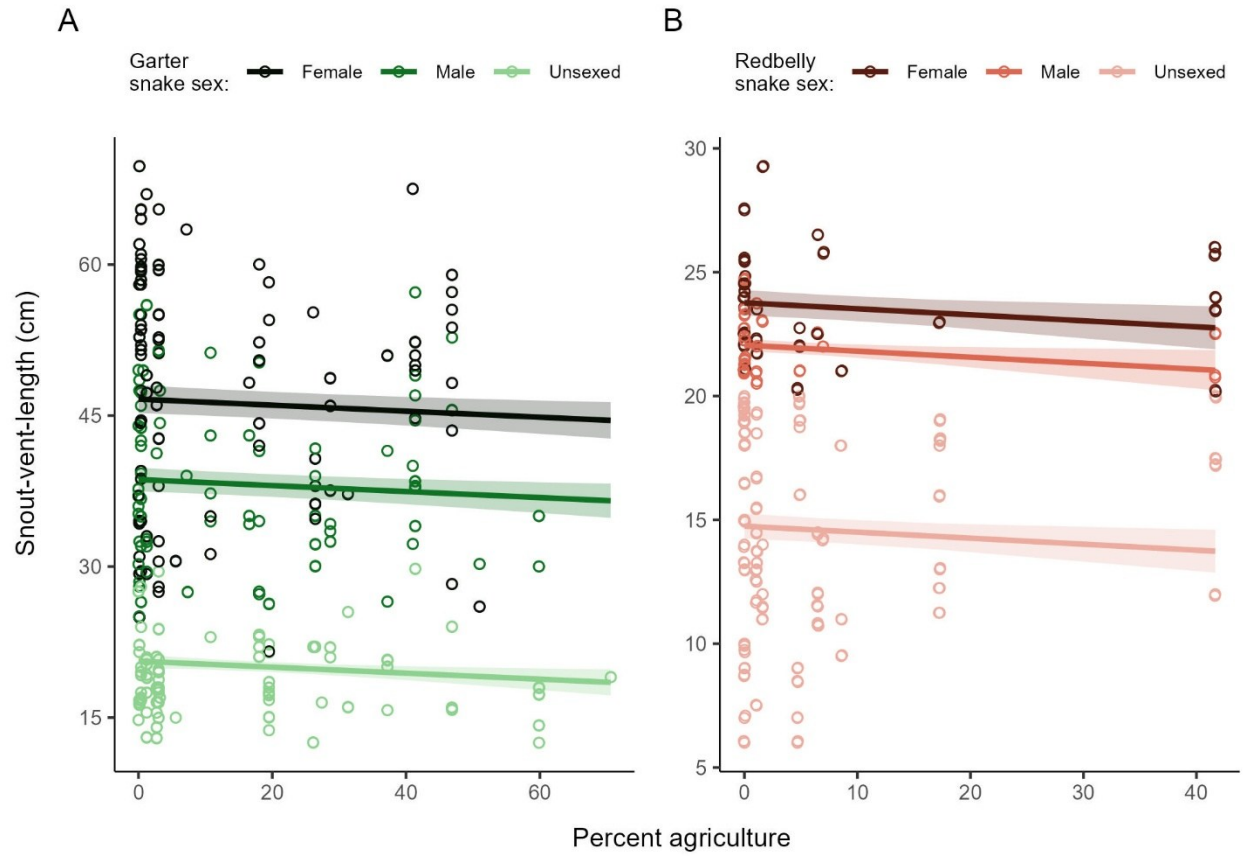


Figure 3: Model-predicted snake size (snout-vent-length; SVL) for garter snakes (A) and redbelly snake (B) versus the percentage of agricultural land cover in the landscape. Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24. Trend lines were predicted from the final selected models including vegetation cover as a predictor.

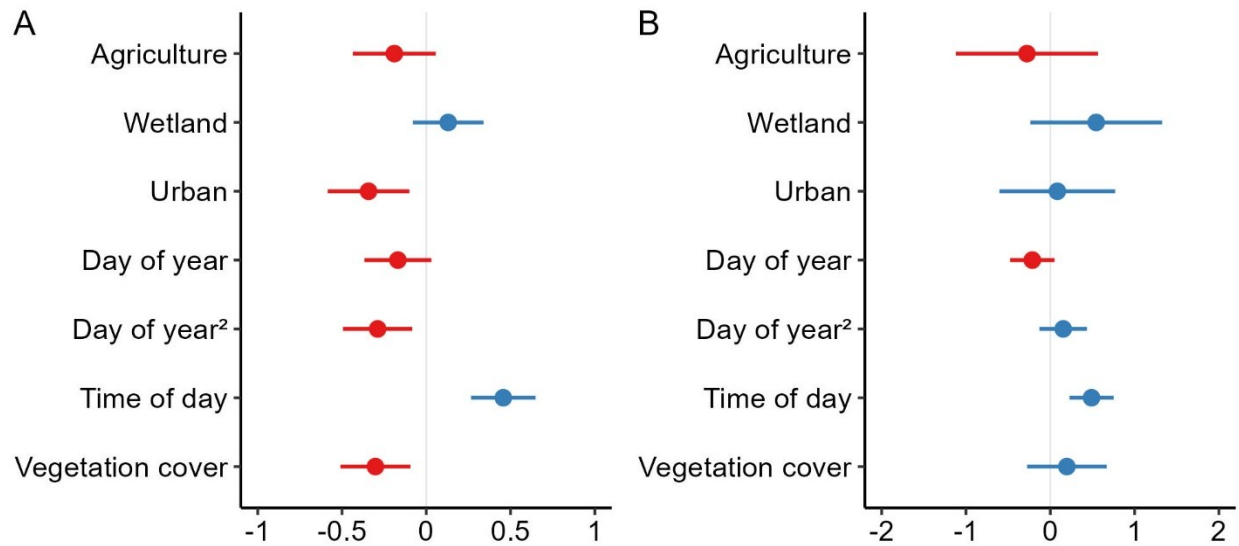


Figure 4: Parameter estimates for the final models including vegetation cover as a predictor for garter snake abundance (A) and redbelly snake abundance (B). Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24.

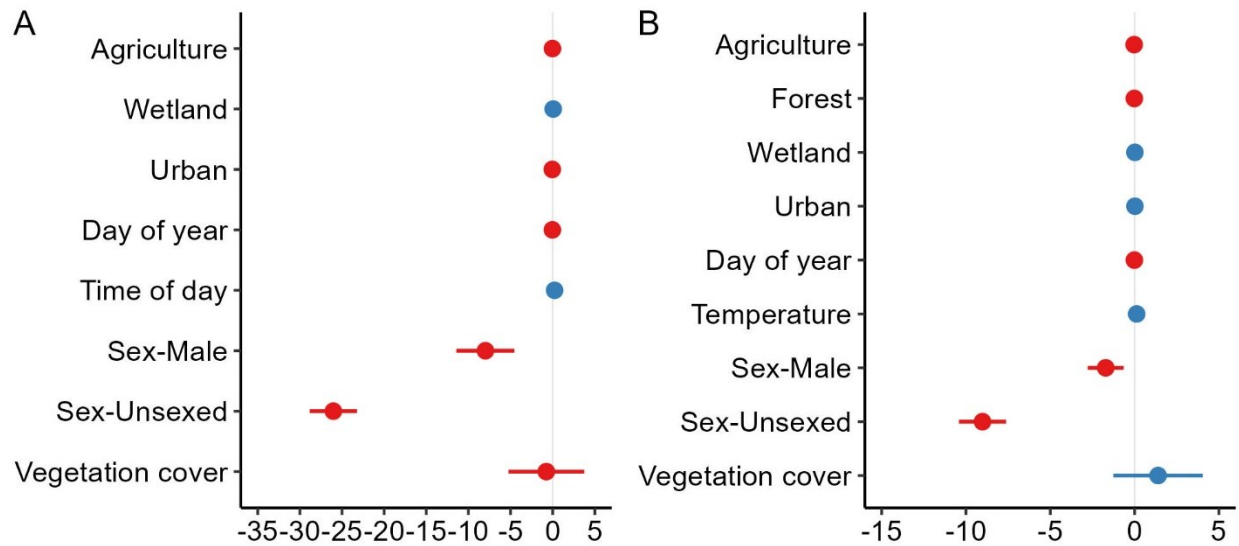


Figure 5: Parameter estimates for the final models including vegetation cover as a predictor for garter snake size (snout-vent-length; SVL; A) and redbelly snake SVL (B). Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24.

Supplementary Information

Appendix 1: Additional statistical information

Table SI 1: Variance inflation factors (VIFs) for garter snake and redbelly snake abundance models. Snake abundance was surveyed at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24.

| Agriculture | Crop | Pasture | Forest | Wetland | Urban | Day of year | Day of year ² | Time of day | Vegetation cover |
|--|------|---------|--------|---------|-------|----------------|-----------------------------|----------------|---------------------|
| Model: Garter snake abundance | | | | | | | | | |
| 1.2 | NA | NA | NA | 1.4 | 1.1 | 1.2 | 1.4 | 1.1 | 1.4 |
| Model: Redbelly snake abundance | | | | | | | | | |
| 2.4 | NA | NA | 3.1 | 2.2 | 1.6 | 1.2 | 1.5 | 1.0 | 1.4 |
| Model: Garter snake abundance (no vegetation cover) | | | | | | | | | |
| 1.2 | NA | NA | NA | 1.2 | 1.0 | 1.1 | 1.1 | 1.1 | NA |
| Model: Redbelly snake abundance (no vegetation cover) | | | | | | | | | |
| 2.4 | NA | NA | 3.1 | 2.3 | 1.7 | 1.1 | 1.1 | 1.0 | NA |
| Model: Garter snake abundance (crop and pasture) | | | | | | | | | |
| NA | 1.1 | 1.4 | NA | 1.5 | 1.1 | 1.2 | 1.4 | 1.1 | 1.4 |
| Model: Redbelly snake abundance (crop and pasture) | | | | | | | | | |
| NA | 1.0 | 1.3 | NA | 1.4 | 1.1 | 1.2 | 1.4 | 1.0 | 1.3 |

Table SI 2: Variance inflation factors for the garter snake and redbelly snake snout-vent-length (SVL) models. Snakes were sampled at 31 sites over an agricultural gradient in Ottawa/Gatineau area from May to September 2023-24.

| Agri- culture | Crop | Pasture | Forest | Wet- land | Urban | Day of year | Time of day | Temper- ature | Sex | Vegetation cover |
|--|------|---------|--------|--------------|-------|----------------|----------------|------------------|-----|---------------------|
| Model: Garter snake SVL | | | | | | | | | | |
| 1.3 | NA | NA | NA | 1.2 | 1.1 | 1.1 | 1.2 | NA | 1.1 | 1.5 |
| Model: Redbelly snake SVL | | | | | | | | | | |
| 1.6 | NA | NA | 1.3 | 2.7 | 1.3 | 1.5 | NA | 1.1 | 1.2 | 2.0 |
| Model: Garter snake SVL (no vegetation cover) | | | | | | | | | | |
| 1.0 | NA | NA | NA | 1.1 | 1.1 | 1.2 | 1.2 | NA | 1.1 | NA |
| Model: Redbelly snake SVL (no vegetation cover) | | | | | | | | | | |
| 1.5 | NA | NA | 1.3 | 1.6 | 1.3 | 1.2 | NA | 1.0 | 1.2 | NA |
| Model: Garter snake SVL (crop and pasture) | | | | | | | | | | |
| NA | 1.3 | 1.4 | NA | 1.6 | 1.2 | 1.1 | 1.2 | NA | 1.1 | 1.5 |
| Model: Redbelly snake SVL (crop and pasture) | | | | | | | | | | |
| NA | 1.1 | 1.4 | NA | 1.7 | 1.2 | 1.2 | NA | 1.1 | 1.2 | 1.5 |

Appendix 2: Land cover and site selection



Figure SI 1: Sample wetlands that were chosen as field sites. I selected 31 total wetlands across a gradient of agricultural to natural landscapes in Ottawa/Gatineau. Sites were selected based on whether they were open (not closed canopy) and had enough dry ground to place a transect. Each site had a 100 m to 200 m transect with 10 to 20 cover boards.

A**B**

Figure SI 2: Photographs of captured individuals for each study species: a garter snake (*Thamnophis sirtalis*; A) and a redbelly snake (*Storeria occipitomaculata*; B).



Figure SI 3: Sample wetland site viewed from ArcGIS Pro. The coordinates of cover boards along the sampling transects are depicted as black circles. I generated 10 random coordinates within a 10 m buffer along each transect to measure vegetation cover (pink circles). A total of 31 wetland sites (10 to 20 cover boards each) were surveyed from May to September 2023-24 across a gradient of agricultural landscapes.

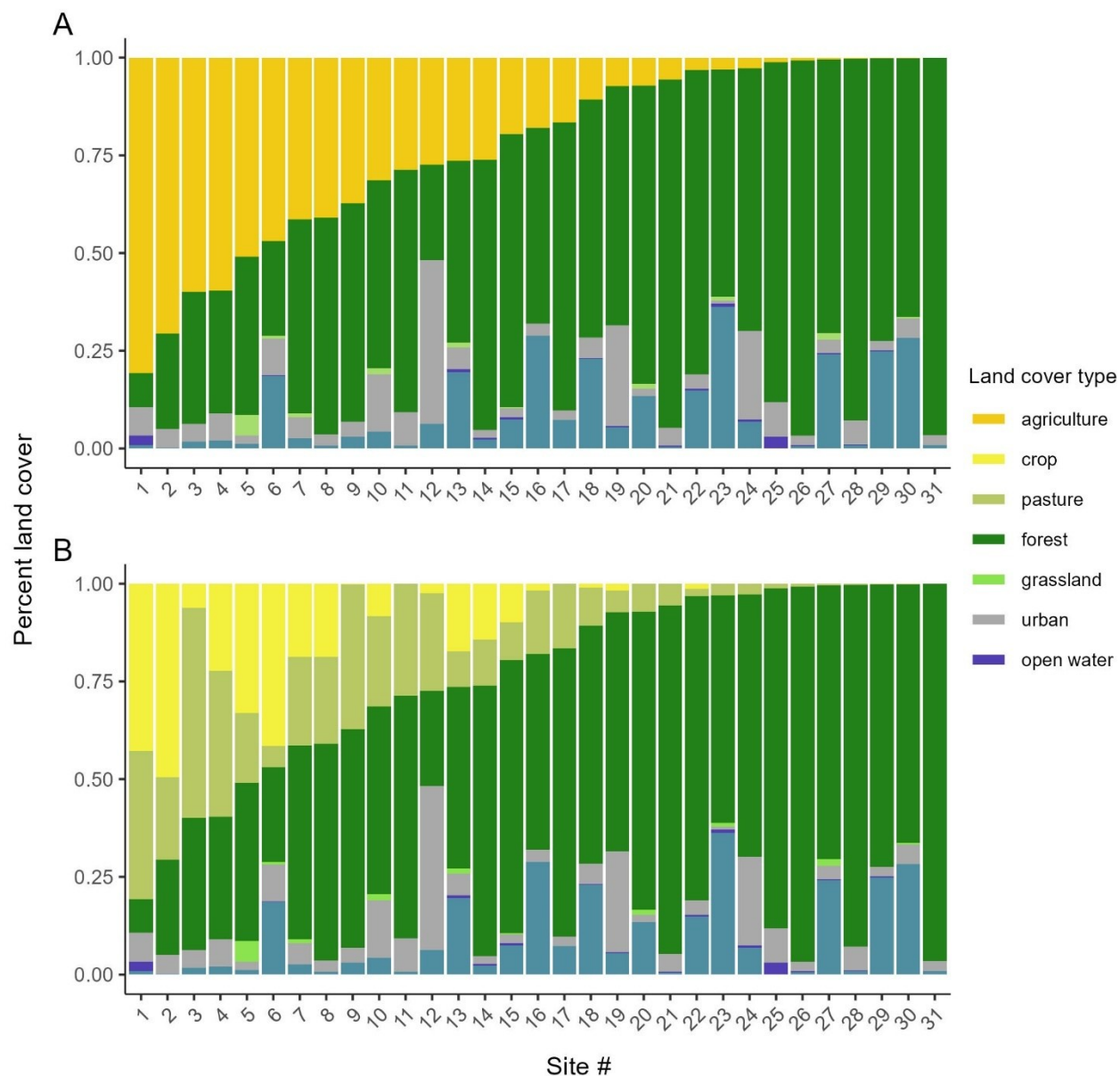


Figure SI 4: Variation in the proportion of the different land covers by site, for 31 wetland sites, using agriculture as the land cover of interest (A), and land cover proportions using crop and pasture as the land covers of interest (B). Sites were selected across a gradient of agricultural landscapes in Ottawa/Gatineau and surveyed from May to September 2023-24. Land covers were classified according to Ontario Land Cover Compilation (OLCC), Comptes des Terres de Québec (CTQ), and Agriculture and Agri-Food Canada Annual Crop Inventory 2021.

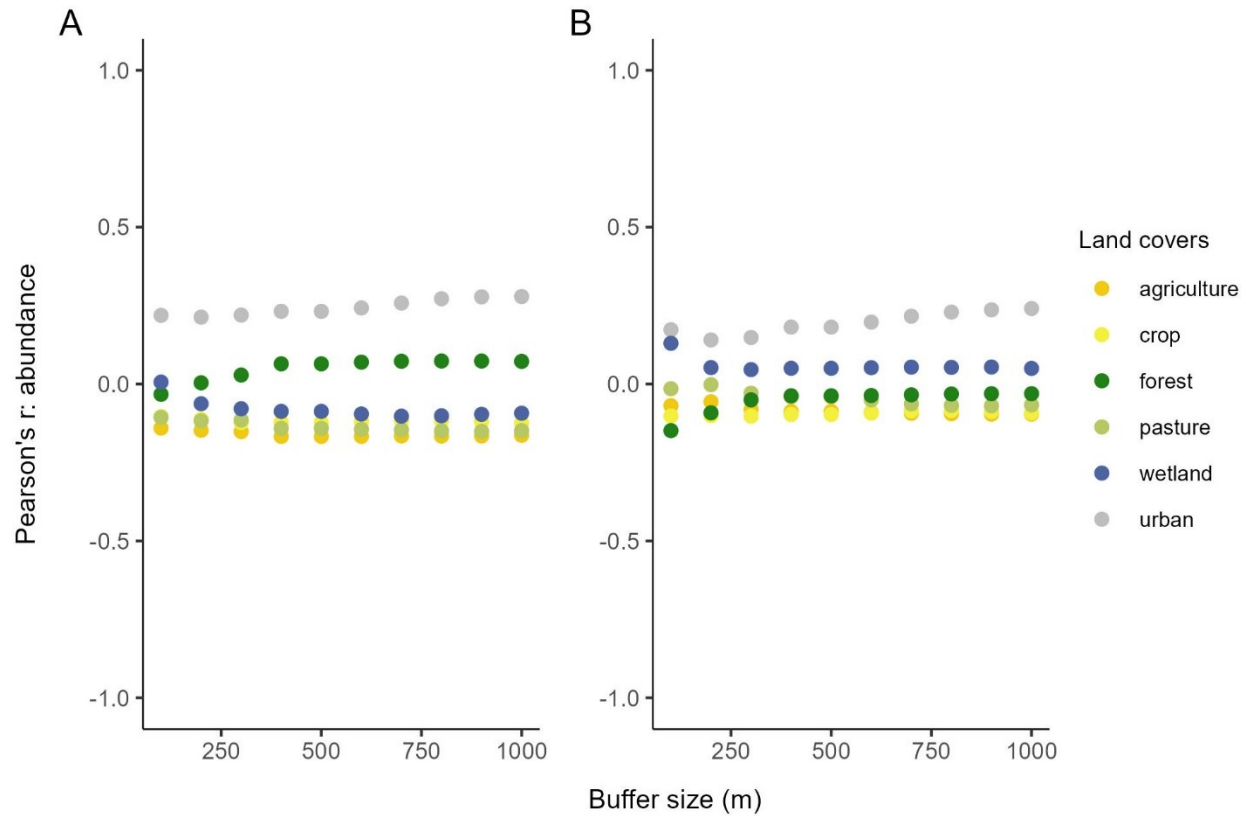


Figure SI 5: Pearson's correlation coefficients for the percentage of the different land covers in the surrounding landscape at different buffer sizes for garter snake abundance (A) and for redbelly snake abundance (B). Buffer sizes ranged from 100 m to 1000 m around each wetland site. Sites were selected across a gradient of agricultural landscapes in Ottawa/Gatineau and surveyed from May to September 2023-24. Land covers were classified according to Ontario Land Cover Compilation (OLCC), Comptes des Terres de Québec (CTQ), and Agriculture and Agri-Food Canada Annual Crop Inventory 2021.

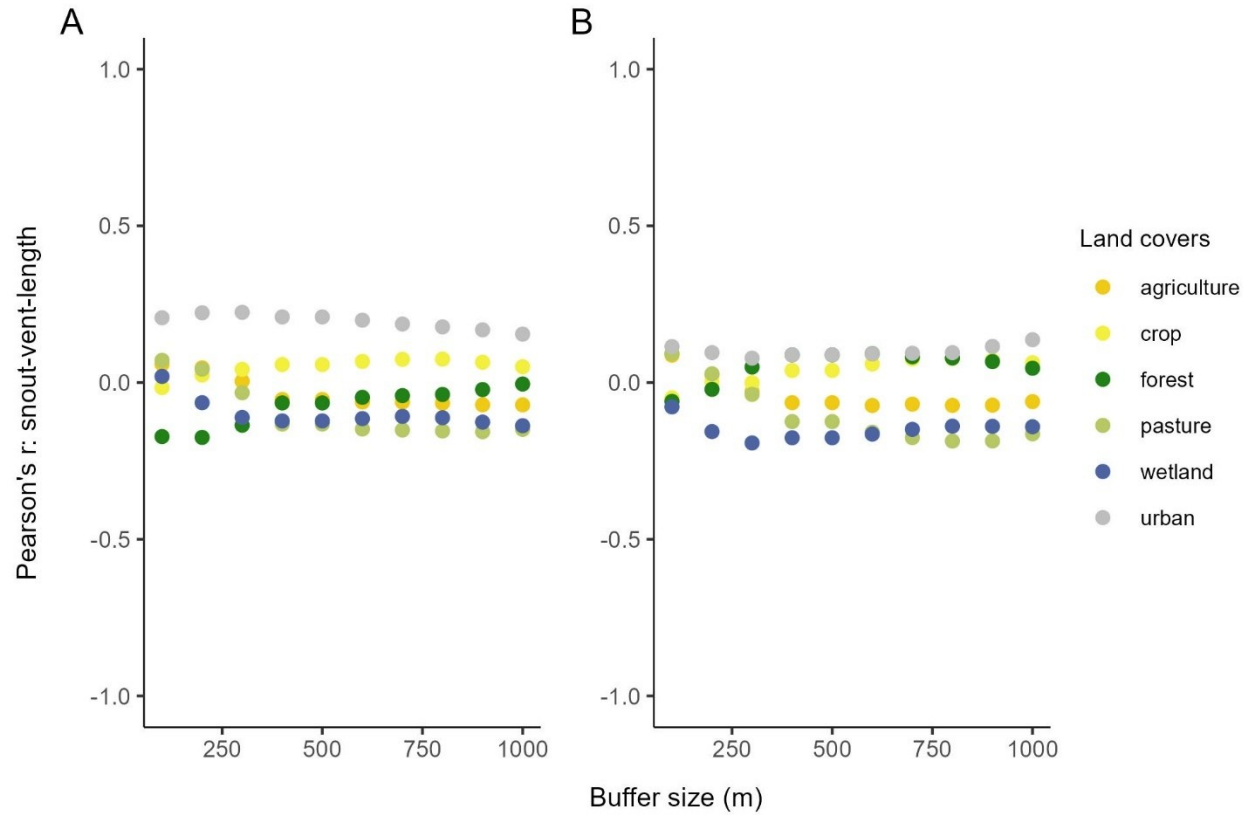


Figure SI 6: Pearson's correlation coefficients for the percentage of the different land covers in the surrounding landscape at different buffer sizes for garter snake snout-vent-length (SVL; A) and for redbelly snake SVL (B). Buffer sizes ranged from 100 m to 1000 m around each wetland site. Sites were selected across a gradient of agricultural landscapes in Ottawa/Gatineau and surveyed from May to September 2023-24. Land covers were classified according to Ontario Land Cover Compilation (OLCC), Comptes des Terres de Québec (CTQ), and Agriculture and Agri-Food Canada Annual Crop Inventory 2021.

Table SI 3: Land cover category re-classification according to the different ArcGIS layers used. The Ontario Land Cover Compilation (OLCC), the Comptes des Terres du Québec (CTQ), and Agriculture and Agri-Food Canada Annual Crop Inventory 2021 layers were used to classify the land covers within 100 m to 1000 m buffers around each site. Sites were selected across a gradient of agricultural landscapes in Ottawa/Gatineau and surveyed from May to September 2023-24.

| Original land cover categories within area | Amalgamated land cover categories |
|---|--|
| OLCC | |
| Clear open water | Water |
| Marsh | Wetland |
| Swamp | Wetland |
| Fen | Wetland |
| Bog | Wetland |
| Sparse treed | Forest |
| Treed upland | Forest |
| Deciduous treed | Forest |
| Mixed treed | Forest |
| Coniferous treed | Forest |
| Plantations – treed cultivated | Forest |
| Community infrastructure | Urban |
| Hedge rows | Agriculture |
| Agriculture and undifferentiated rural | Agriculture |
| CTQ | |
| Artificial surface | Urban |
| Agriculture | Agriculture |
| Forested wetland | Wetland |
| Herbaceous or shrubby wetland | Wetland |
| Water bodies | Open water |
| Coniferous forest | Forest |
| Deciduous forest | Forest |
| Mixed forest | Forest |
| Open canopy forest | Forest |
| AAFC Crop Inventory 2021 | |
| Winter wheat | Crop |
| Spring wheat | Crop |
| Barley | Crop |
| Millet | Crop |
| Oats | Crop |
| Rye | Crop |
| Spelt | Crop |
| Sorghum | Crop |
| Quinoa | Crop |
| Buckwheat | Crop |
| Canola/rapeseed | Crop |
| Sunflower | Crop |
| Soybeans | Crop |
| Hemp | Crop |
| Peas | Crop |

| | |
|------------------|------------|
| Beans | Crop |
| Corn | Crop |
| Potatoes | Crop |
| Other vegetables | Crop |
| Blueberry | Crop |
| Cranberry | Crop |
| Other berry | Crop |
| Other crops | Crop |
| Pasture/forages | Pasture |
| Sod | Pasture |
| Grassland | Grassland |
| Shrubland | Grassland |
| Wetland | Wetland |
| Water | Open water |
| Nursery | Forest |
| Orchards | Fores |
| Coniferous | Forest |
| Broadlead | Forest |
| Mixedwood | Forest |
| Urban/developed | Urban |
| Greenhouses | Urban |

Appendix 3: Data exploration and trends

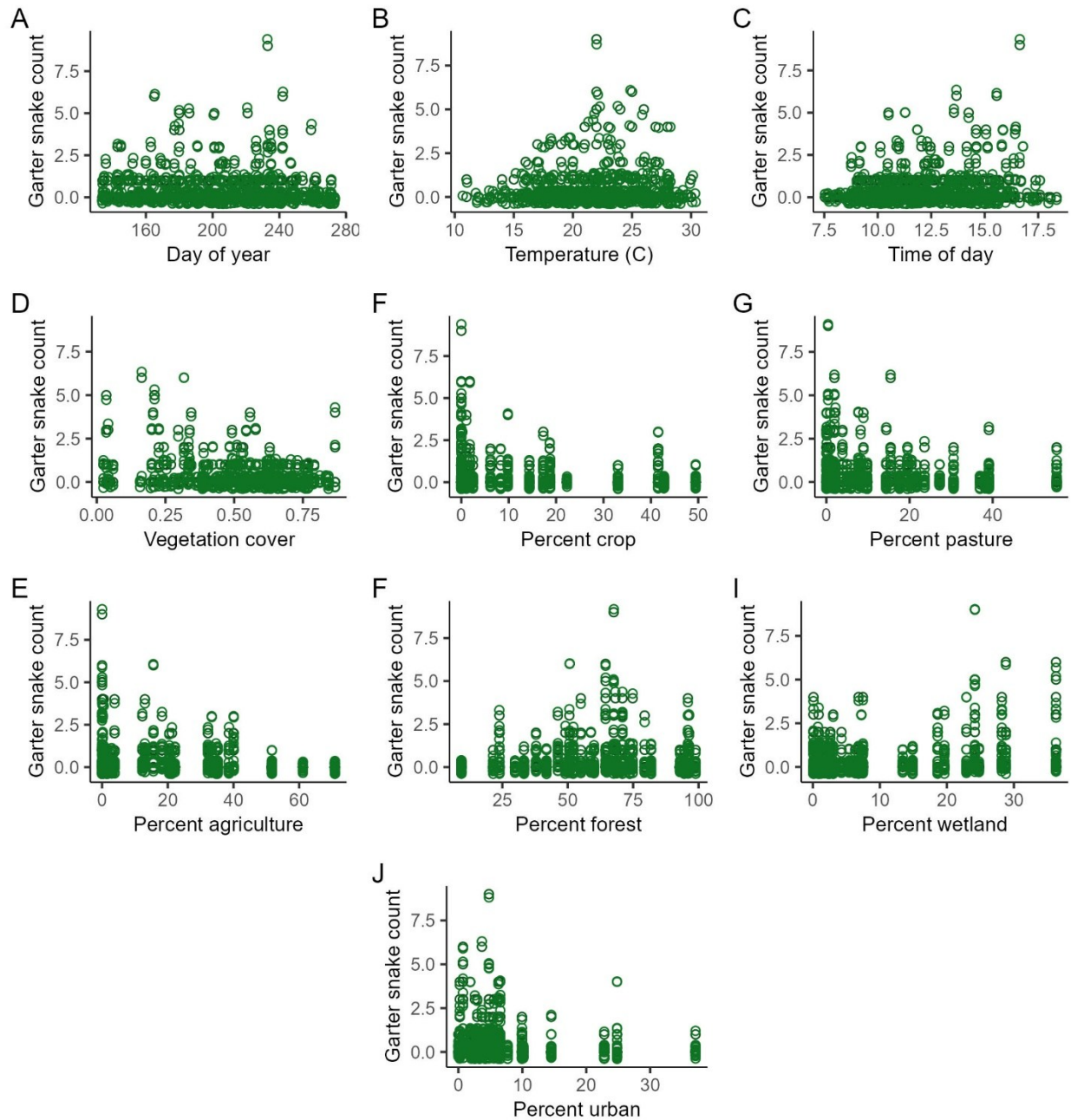


Figure SI 7: Garter snake abundance plotted against each predictor variable tested. Snake abundance was surveyed at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24. Data points were jittered to distinguish overlapping points.

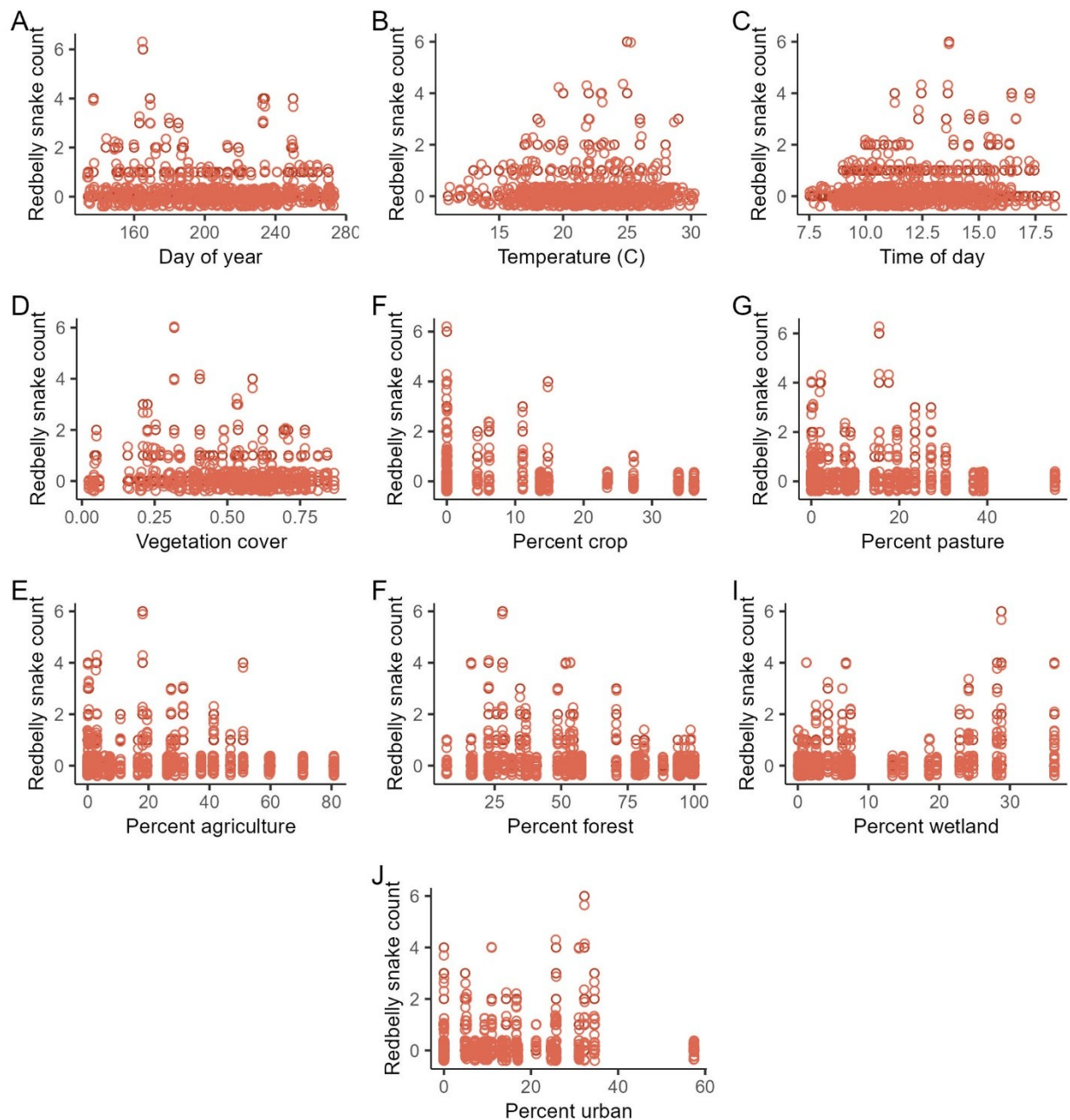


Figure SI 8: Redbelly snake abundance plotted against each predictor variable tested. Snake abundance was surveyed at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24. Data points were jittered to distinguish overlapping points.

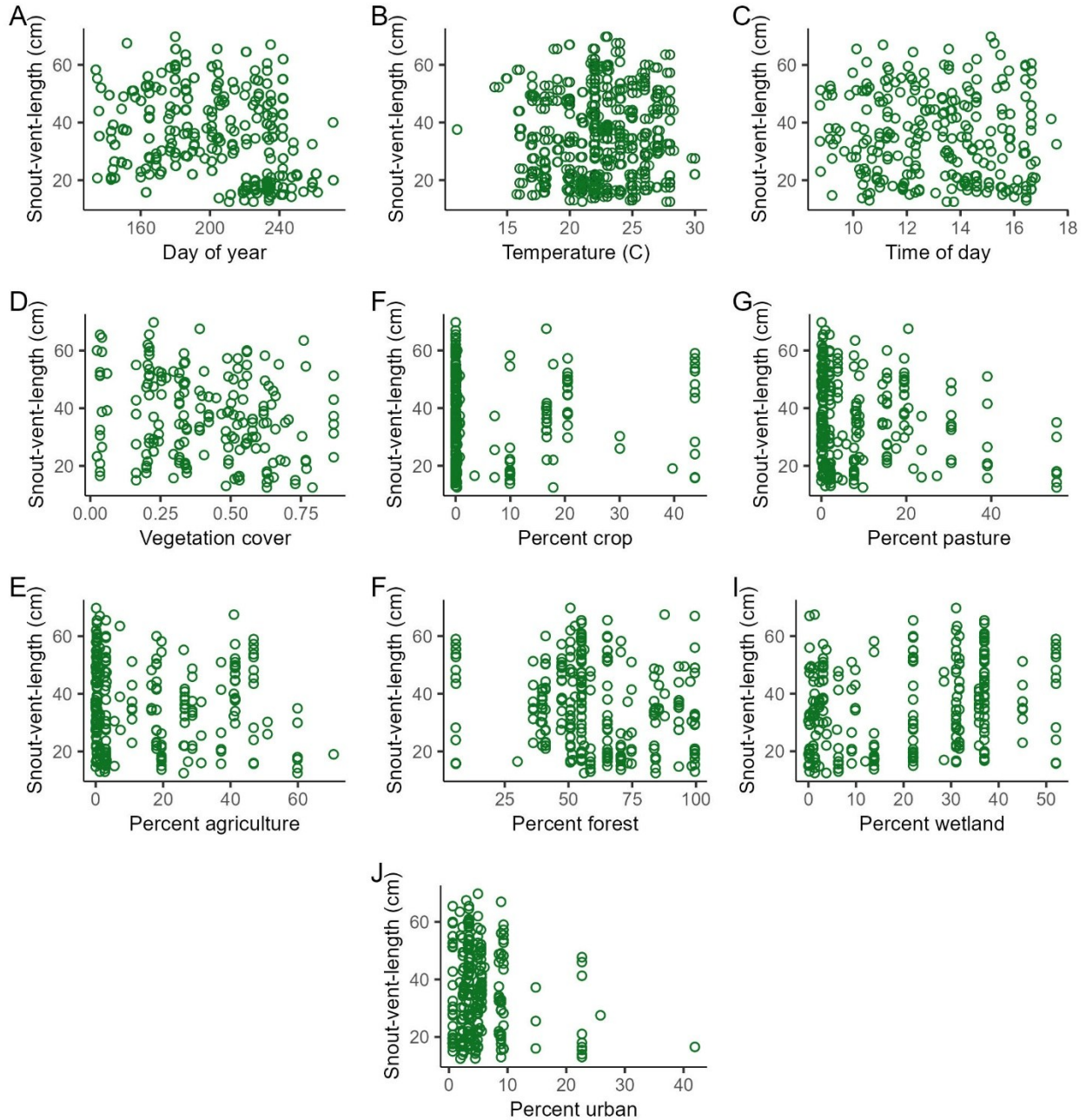


Figure SI 9: Garter snake snout-vent-length (SVL) plotted against each predictor variable tested. Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24. Data points were jittered to distinguish overlapping points.

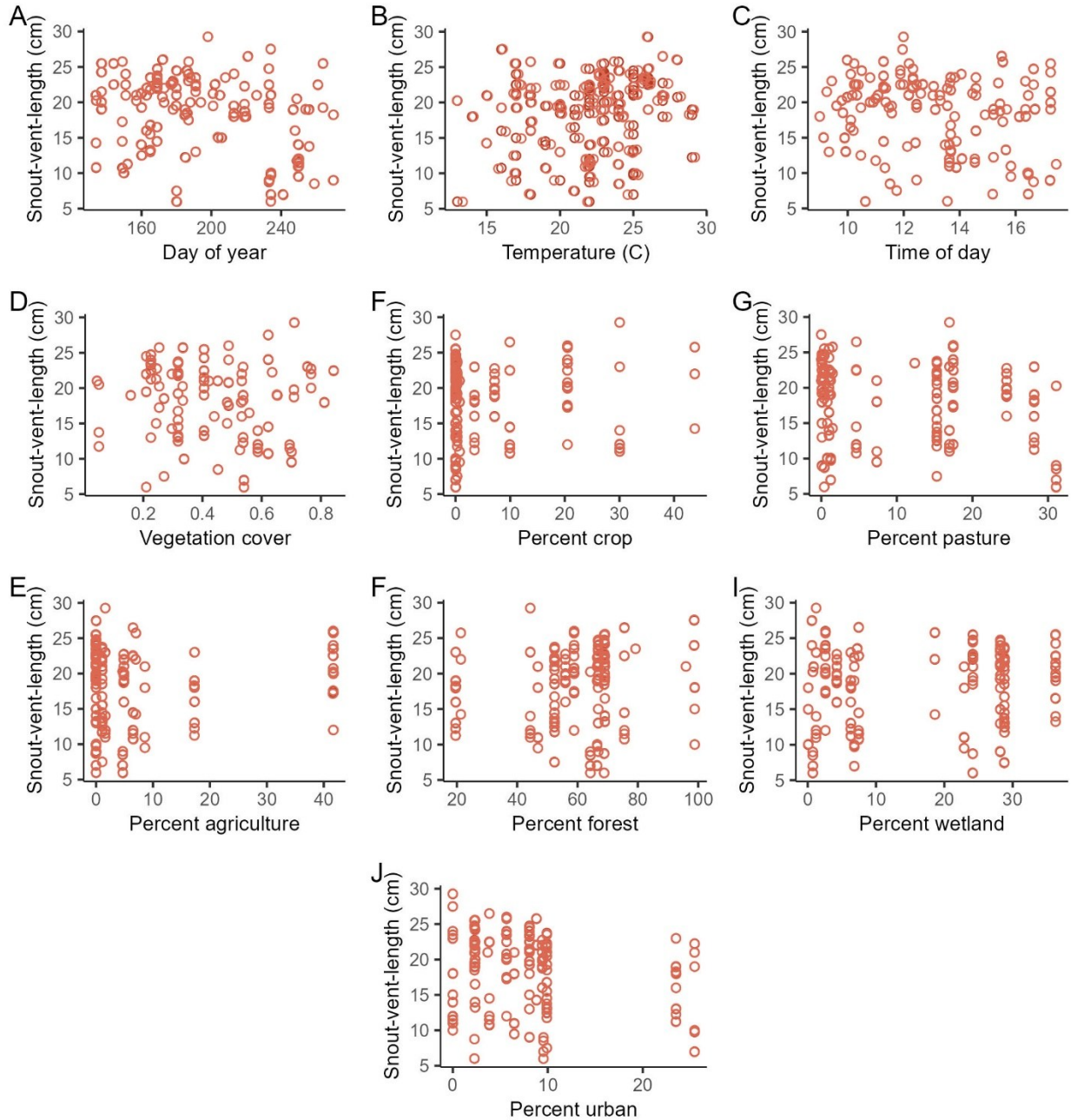


Figure SI 10: Redbelly snake snout-vent-length (SVL) plotted against each predictor variable tested. Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24. Data points were jittered to distinguish overlapping points.

Appendix 4: Alternative models' output

Table SI 4: Summary statistics for the reduced generalized linear mixed models using the full dataset for both years, without vegetation cover as a predictor for garter and redbelly snake abundance. Snake abundance was surveyed at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24. Variables are on a log scale and were centred and scaled.

| Model: Garter snake abundance (no vegetation cover) | | | | | |
|--|----------|----------------|---------|---------|-----|
| Parameter | Estimate | Standard error | z value | p-value | |
| (Intercept) | -3.82 | 0.17 | -22.21 | < 0.00 | *** |
| Agriculture (400m) | -0.38 | 0.17 | -2.22 | 0.03 | * |
| Wetland (1000m) | 0.24 | 0.15 | 1.61 | 0.11 | |
| Urban (700m) | -0.31 | 0.16 | -1.99 | 0.05 | * |
| Day of year | -0.13 | 0.09 | -1.47 | 0.14 | |
| Day of year ² | -0.24 | 0.09 | -2.82 | < 0.00 | ** |
| Time of day | 0.51 | 0.09 | 5.91 | < 0.00 | *** |
| Model: Redbelly snake abundance (no vegetation cover) | | | | | |
| Parameter | Estimate | Standard error | z value | p-value | |
| (Intercept) | -5.45 | 0.41 | -13.38 | < 0.00 | *** |
| Agriculture (1000m) | -0.31 | 0.40 | -0.77 | 0.44 | |
| Forest (100m) | 0.48 | 0.36 | 1.35 | 0.18 | |
| Wetland (1000m) | 0.15 | 0.32 | 0.47 | 0.64 | |
| Urban (100m) | -0.23 | 0.11 | -2.12 | 0.03 | * |
| Day of year | 0.03 | 0.11 | 0.29 | 0.77 | |
| Day of year ² | 0.52 | 0.12 | 4.51 | < 0.00 | *** |
| Time of day | -5.45 | 0.41 | -13.38 | < 0.00 | *** |

Table SI 5: Summary statistics for the reduced generalized linear mixed models looking at crop and pasture separately rather than “agriculture” more broadly, for garter and redbelly snake abundance. Snake abundance was surveyed at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24. Variables are on a log scale and were centred and scaled.

| Model: Garter snake abundance (crop and pasture) | | | | | |
|--|----------|----------------|---------|---------|-----|
| Parameter | Estimate | Standard error | z value | p-value | |
| (Intercept) | -3.60 | 0.15 | -23.43 | < 0.00 | *** |
| Crop (1000m) | -0.15 | 0.12 | -1.24 | 0.22 | |
| Pasture (900m) | -0.04 | 0.12 | -0.38 | 0.71 | |
| Wetland (1000m) | 0.15 | 0.12 | 1.30 | 0.19 | |
| Urban (700m) | -0.36 | 0.13 | -2.89 | 0.00 | ** |
| Day of year | -0.17 | 0.10 | -1.68 | 0.09 | . |
| Day of year ² | -0.29 | 0.11 | -2.77 | 0.01 | ** |
| Time of day | 0.46 | 0.10 | 4.67 | < 0.00 | *** |
| Vegetation cover | -0.30 | 0.11 | -2.83 | < 0.00 | ** |
| Model: Redbelly snake abundance (no vegetation cover) | | | | | |
| Parameter | Estimate | Standard error | z value | p-value | |
| (Intercept) | -5.62 | 0.47 | -11.95 | < 0.00 | *** |
| Crop (300m) | -0.43 | 0.40 | -1.08 | 0.28 | |
| Pasture (900m) | -0.12 | 0.41 | -0.29 | 0.78 | |
| Wetland (1000m) | 0.54 | 0.40 | 1.36 | 0.18 | |
| Urban (100m) | 0.12 | 0.34 | 0.35 | 0.73 | |
| Day of year | -0.21 | 0.13 | -1.58 | 0.12 | |
| Day of year ² | 0.16 | 0.14 | 1.10 | 0.27 | |
| Time of day | 0.49 | 0.13 | 3.63 | < 0.00 | *** |
| Vegetation cover | 0.21 | 0.24 | 0.88 | 0.38 | |

Table SI 6: Summary statistics for the alternative linear mixed models using the full dataset for both years, without vegetation cover as a predictor for garter snake and redbelly snake size (snout-vent-length; SVL). Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24.

| Model: Garter snake SVL (without vegetation cover) | | | | | | |
|---|----------|----------------|--------|---------|---------|-----|
| Parameter | Estimate | Standard error | DF | t-value | p-value | |
| (Intercept) | 54.50 | 3.05 | 220.00 | 17.88 | < 0.00 | *** |
| Agriculture (1000m) | -0.01 | 0.02 | 24.00 | -0.57 | 0.57 | |
| Wetland (300m) | 0.02 | 0.03 | 24.00 | 0.78 | 0.45 | |
| Urban (1000m) | -0.08 | 0.07 | 24.00 | -1.23 | 0.23 | |
| Day of year | -0.03 | 0.01 | 220.00 | -2.70 | 0.01 | * |
| Time of day | -0.12 | 0.17 | 220.00 | -0.72 | 0.47 | |
| Sex (Male) | -8.34 | 1.52 | 220.00 | -5.47 | < 0.00 | *** |
| Sex (Unsexed) | -26.84 | 1.28 | 220.00 | -20.91 | < 0.00 | *** |
| Model: Redbelly snake SVL (without vegetation cover) | | | | | | |
| Parameter | Estimate | Standard error | DF | t-value | p-value | |
| (Intercept) | 22.74 | 1.99 | 113 | 11.44 | < 0.00 | *** |
| Agriculture (100m) | 0.01 | 0.02 | 12 | 0.30 | 0.77 | |
| Forest (600 m) | -0.01 | 0.01 | 12 | -0.79 | 0.45 | |
| Wetland (1000m) | 0.01 | 0.02 | 12 | 0.56 | 0.59 | |
| Urban (300m) | -0.06 | 0.04 | 12 | -1.72 | 0.11 | |
| Day of year | 0.00 | 0.01 | 113 | 0.75 | 0.45 | |
| Temperature (C) | 0.04 | 0.05 | 113 | 0.81 | 0.42 | |
| Sex (Male) | -1.46 | 0.44 | 113 | -3.34 | < 0.00 | ** |
| Sex (Unsexed) | -8.88 | 0.62 | 113 | -14.24 | < 0.00 | *** |

Table SI 7: Summary statistics for the linear mixed model looking at crop and pasture separately from “agriculture” for garter and redbelly snake size (snout-vent-length; SVL). Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24.

| Model: Garter snake SVL (crop and pasture) | | | | | | |
|---|----------|----------------|--------|---------|---------|-----|
| Parameter | Estimate | Standard error | DF | t-value | p-value | |
| (Intercept) | 50.58 | 3.54 | 156.00 | 14.31 | < 0.00 | *** |
| Crop (800m) | -0.04 | 0.04 | 23.00 | -1.03 | 0.31 | |
| Pasture (900m) | -0.03 | 0.03 | 23.00 | -0.97 | 0.34 | |
| Wetland (300m) | 0.06 | 0.03 | 23.00 | 2.04 | 0.05 | * |
| Urban (1000m) | -0.04 | 0.07 | 23.00 | -0.66 | 0.51 | |
| Day of year | -0.04 | 0.01 | 156.00 | -3.36 | < 0.00 | ** |
| Time of day | 0.22 | 0.21 | 156.00 | 1.08 | 0.28 | |
| Sex (Male) | -8.01 | 1.74 | 156.00 | -4.59 | < 0.00 | *** |
| Sex (Unsexed) | -26.04 | 1.43 | 156.00 | -18.21 | < 0.00 | *** |
| Vegetation cover | -0.63 | 2.29 | 156.00 | -0.28 | 0.78 | |
| Model: Redbelly snake SVL (crop and pasture) | | | | | | |
| Parameter | Estimate | Standard error | DF | t-value | p-value | |
| (Intercept) | 20.27 | 2.35 | 81.00 | 8.63 | 0.00 | *** |
| Crop (800m) | 0.04 | 0.03 | 11.00 | 1.20 | 0.26 | |
| Pasture (800m) | -0.06 | 0.04 | 11.00 | -1.49 | 0.16 | |
| Wetland (1000m) | 0.02 | 0.04 | 11.00 | 0.64 | 0.54 | |
| Urban (300m) | 0.05 | 0.06 | 11.00 | 0.85 | 0.42 | |
| Day of year | 0.00 | 0.01 | 81.00 | -0.50 | 0.62 | |
| Temperature (C) | 0.13 | 0.06 | 81.00 | 2.11 | 0.04 | * |
| Sex (Male) | -1.89 | 0.53 | 81.00 | -3.60 | 0.00 | *** |
| Sex (Unsexed) | -8.80 | 0.67 | 81.00 | -13.06 | 0.00 | *** |
| Vegetation cover | 1.70 | 1.97 | 81.00 | 0.86 | 0.39 | |

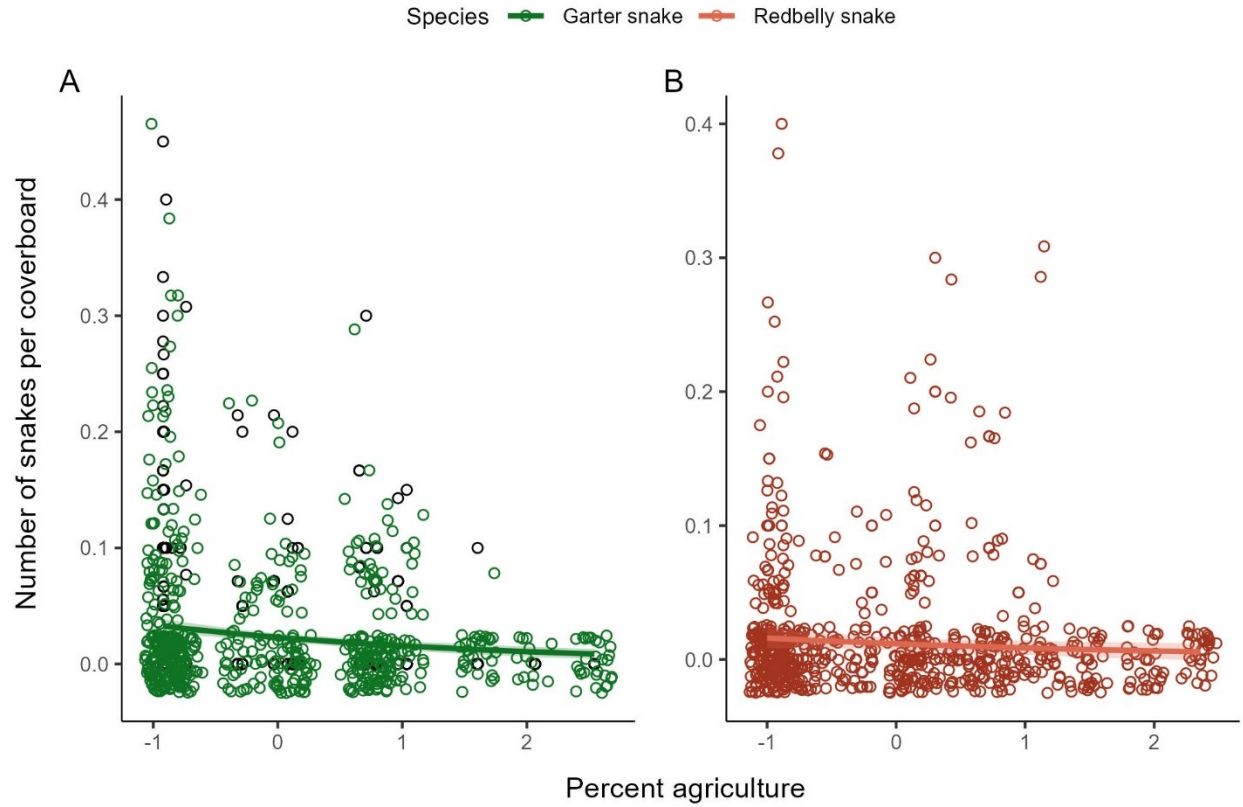


Figure SI 11: Model-predicted garter snake abundance (A) and redbelly abundance (B) versus the percentage of agricultural land cover in the landscape. Trend lines were predicted from the alternative models without vegetation cover, using the full dataset for both years. Snake abundance was surveyed at 31 wetland sites across an agricultural gradient in Ottawa/Gatineau from May to September 2023-24.

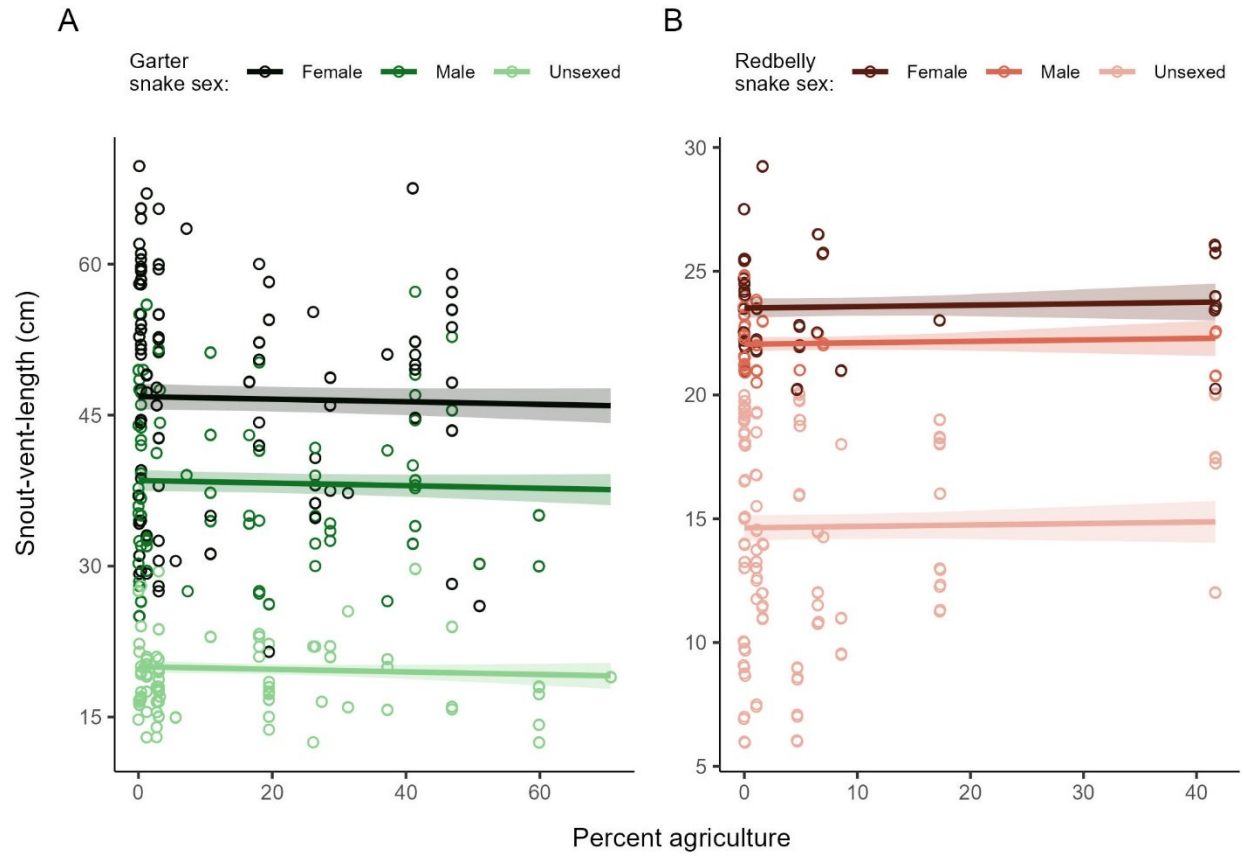


Figure SI 12: Model-predicted snake snout-vent-length (SVL) for garter snakes (A) and redbelly snake (B) versus the percentage of agricultural land cover in the landscape. Trend lines were predicted from the alternative models using the full data set without vegetation cover as a predictor. Snakes were sampled at 31 wetland sites across an agricultural gradient in Ottawa/Gatineau from May to September 2023-24.

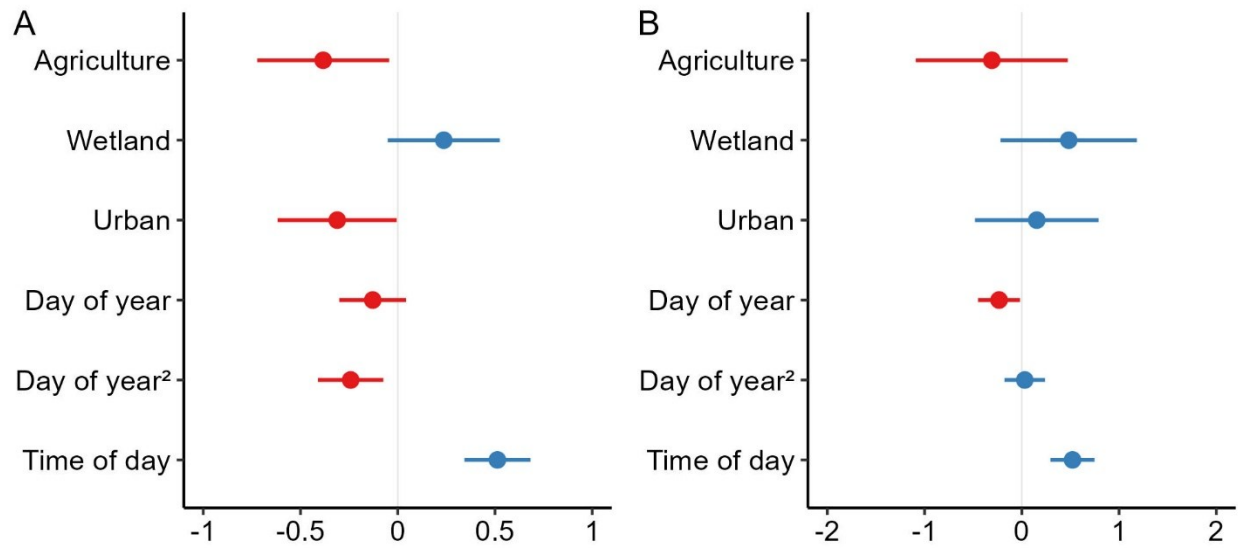


Figure SI 13: Parameter estimates from the alternative models using the full dataset without vegetation cover as a predictor for garter snake abundance (A) and redbelly snake abundance (B). Snake abundance was surveyed at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24.

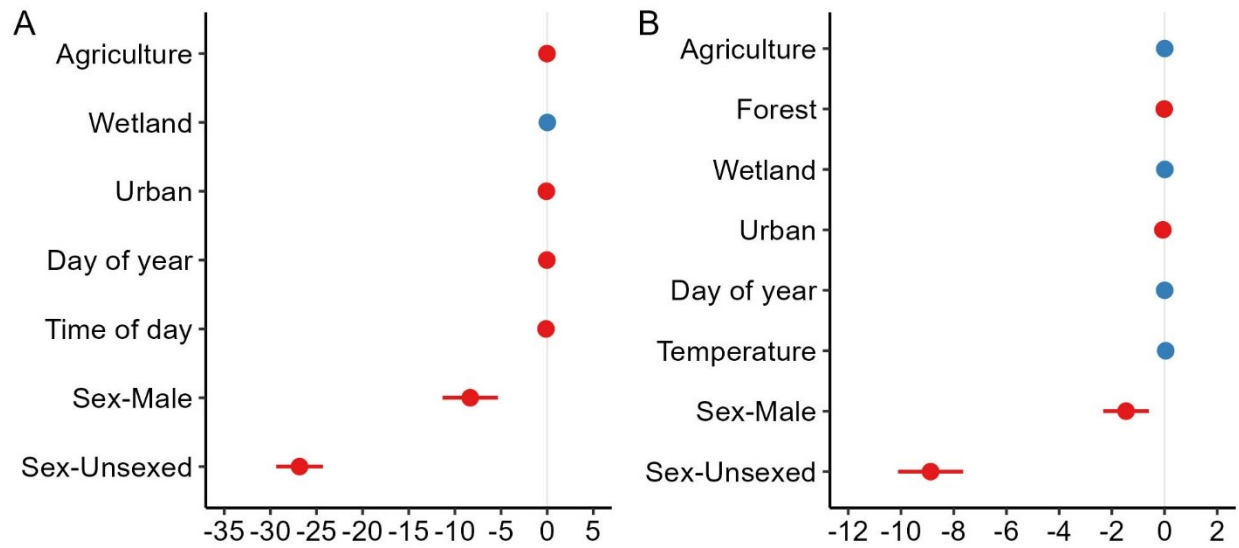


Figure SI 14: Parameter estimates from the models using the full dataset without vegetation cover as a predictor for garter snake snout-vent-length (SVL; A) and redbelly snake SVL (B). Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24.

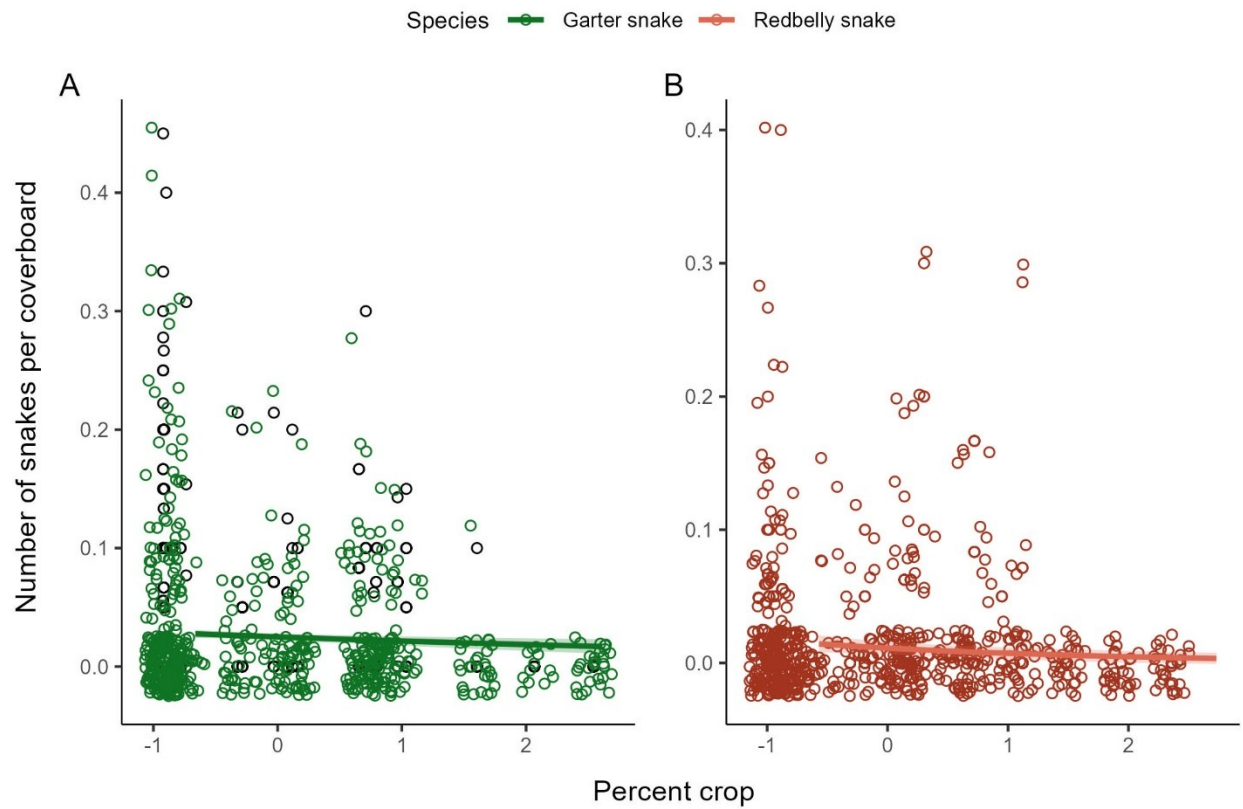


Figure SI 15: Model-predicted garter snake abundance (A) and redbelly abundance (B) versus the percentage of agricultural land cover in the landscape. Trend lines were predicted from the models looking at crop and pasture separately, instead of “agriculture” more broadly. Snake abundance was surveyed at 31 wetland sites across an agricultural gradient in Ottawa/Gatineau from May to September 2023-24.

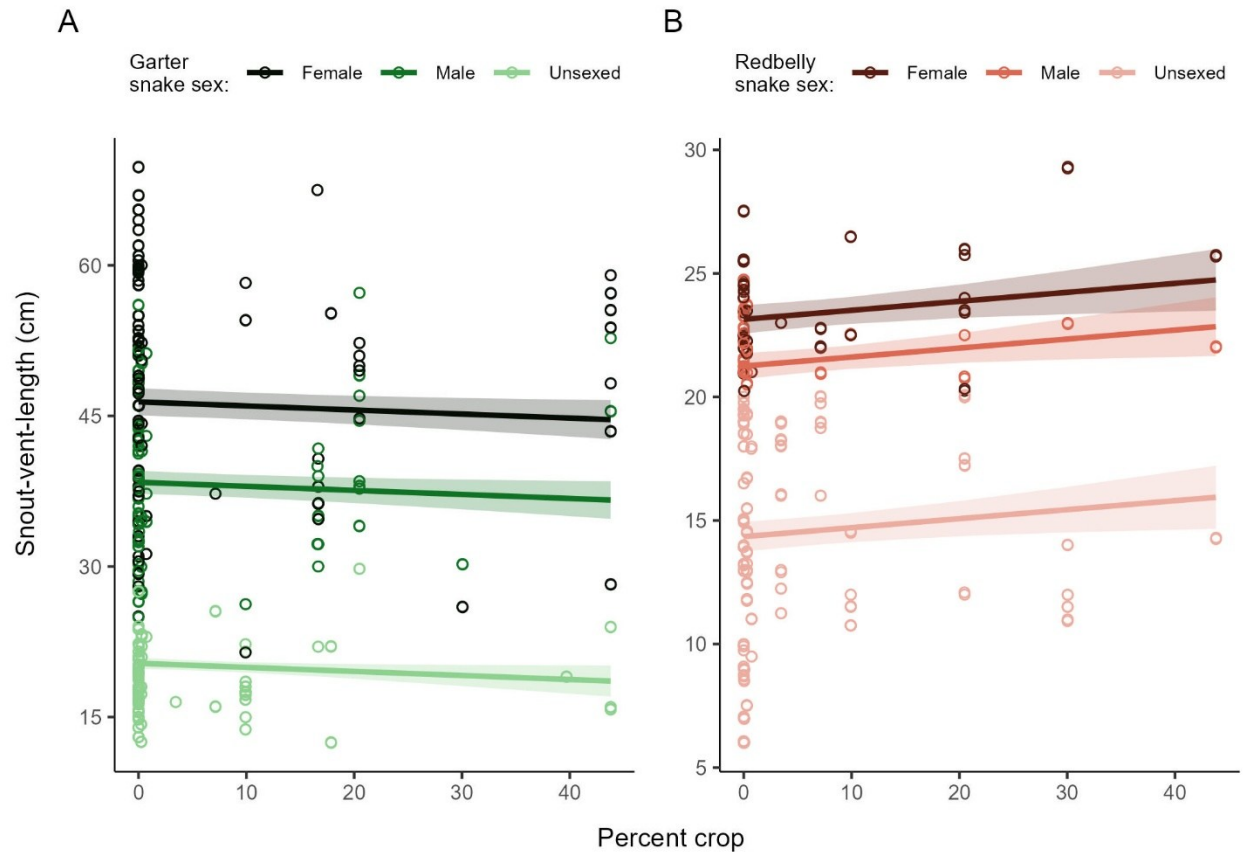


Figure SI 16: Model-predicted snake snout-vent-length (SVL) for garter snakes (A) and redbelly snake (B) versus the percentage of crop cover in the landscape. Trend lines were predicted from the models looking at crop and pasture separately instead of “agriculture” more broadly. Snakes were sampled at 31 wetland sites across an agricultural gradient in Ottawa/Gatineau from May to September 2023-24.

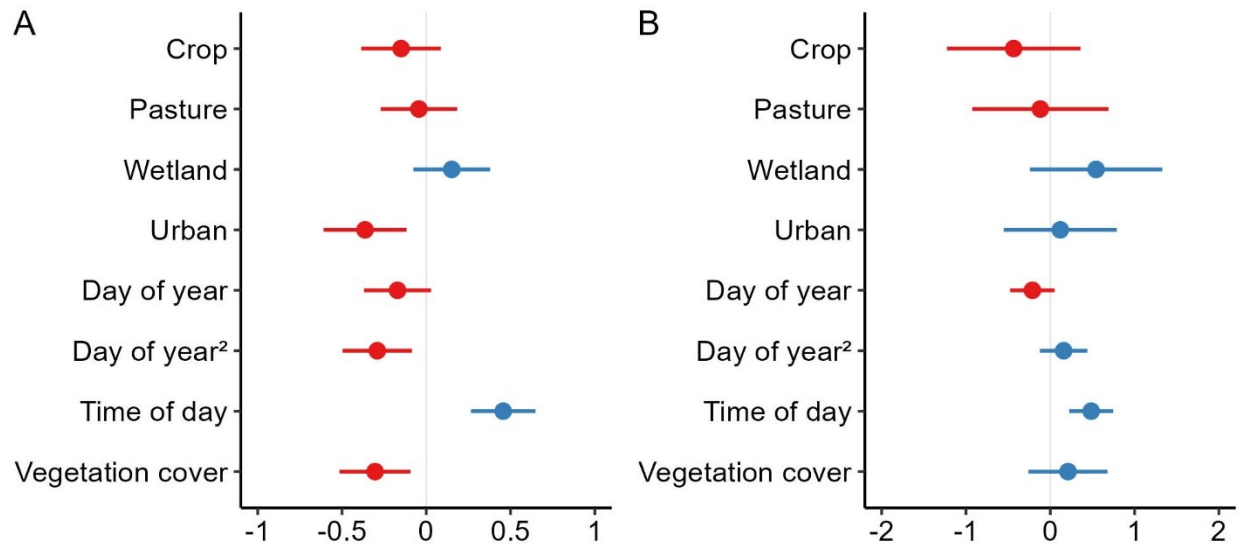


Figure SI 17: Parameter estimates from the models looking at crop and pasture separately, instead of “agriculture” more broadly, for garter snake abundance (A) and redbelly snake abundance (B). Snake abundance was surveyed at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24.

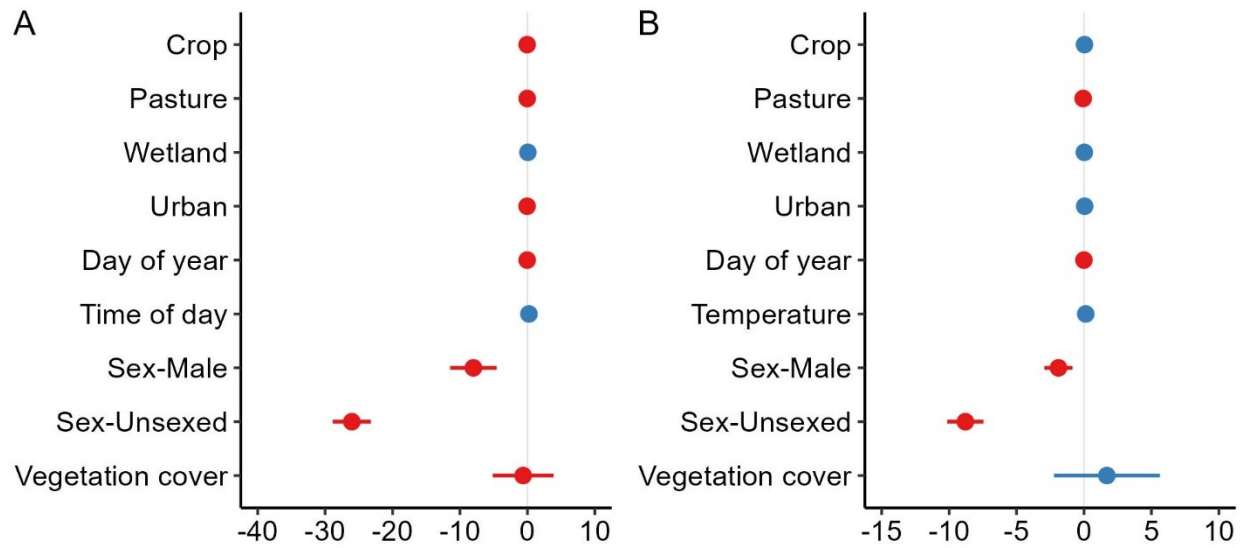


Figure SI 18: Parameter estimates from the models looking at crop and pasture separately, instead of “agriculture” more broadly, for garter snake snout-vent-length (SVL; A) and redbelly snake SVL (B). Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in Ottawa/Gatineau from May to September 2023-24.