Canadian Journal of Zoology

Research Article

Effects of landscape composition on snake abundance and size in wetlands

Michelle L. LaFlamme and **Gabriel Blouin-Demers**

University of Ottawa (Biology Department), Ottawa, ON, Canada

Corresponding author: **Michelle L. LaFlamme** (email: michelle.laflamme@alumni.utoronto.ca)

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Abstract

Habitat loss is driving the biodiversity crisis, and agriculture is one of the leading sources of habitat loss. Reptiles are especially sensitive to environmental change, yet are relatively infrequently studied in this context. We investigated the effects of agriculture in the landscape on garter snake (*Thamnophis sirtalis*; (Linnaeus, 1758)) and redbelly snake (*Storeria occipitomaculata*; Storer, 1839) abundance and size in wetlands in the Gatineau/Ottawa area, Canada. We expected snakes to be less abundant and smaller in wetlands with more agricultural land in the surrounding landscape. We equipped wetlands with coverboards and we visited them once a week from May to September in 2023 and 2024. We found some evidence that snakes were less abundant in wetlands surrounded by more agriculture, but no evidence that they were smaller.

Key words: land management, farmland, land-use, gartersnake, redbellied snake

Introduction

The biodiversity 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 (Pimm et al. 2014; Ceballos et al. 2015; IPBES 2019). Habitat destruction is the main cause of biodiversity loss in terrestrial ecosystems (Newbold et al. 2015; IPBES 2019), with the conversion of natural landscapes to agriculture being one of the leading sources (Newbold et al. 2015; Balouch et al. 2022; Cox et al. 2022; Tan et al. 2023).

Reptiles seem to be particularly sensitive to the impacts of land use change (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). While reptiles 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 (Doherty et al. 2020; Tan et al. 2023).

The literature on the response of reptiles to agriculture is mixed. Some studies suggest a negative impact of agriculture on reptiles (Doherty et al. 2020), showing reduced distribution (Guiller et al. 2022), declining abundance (Reading and Jofré 2015; Guiller et al. 2022), lower species richness and diversity (Ribeiro et al. 2009; Wasiolka and Blaum 2011; Nopper et al. 2017), 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 equally 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, showing no effect of livestock removal on species richness, abundance, and composition in one of two habitat types (Haby and Brandle 2018), no effect of isolated habitat patches in agricultural lands on reptile species richness and abundance (Schutz and Driscoll 2008; Jellinek et al. 2014), no significant differences in species richness and 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; Wisler et al. 2008; Pulsford et al. 2018).

There are several potential mechanisms through which agriculture could negatively affect snakes: (1) Farmland could be an unfavourable habitat for snakes (Row et al. 2012; Marshall et al. 2020), resulting in smaller populations in smaller habitat patches (MacArthur and Wilson 1967). (2) Snakes may suffer direct mortality from agricultural machinery, as has been documented 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; snake-human conflicts are well documented (Whitaker and Shine 2000; Marshall et al. 2018; de Vera et al. 2024).

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;

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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 or tolerate the altered landscape (Wisler et al. 2008; Pulsford et al. 2018). 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 component for snakes and is a major driver of habitat selection, especially in colder climates (Harvey and Weatherhead 2006; Row and Blouin-Demers 2006; Diaz and Blouin-Demers 2017). In contrast, in warmer environments, where optimal temperatures are easier to maintain, other factors, like prey availability or predator avoidance, might play a larger role in dictating habitat selection. Thus, the response to changing landscapes may also differ in different regions. Most studies on reptile response to landscape modification took place in the more southerly regions of the World (Doherty et al. 2020). Most of the studies on snakes were conducted in Australia and assessed the impacts of grazing (Schutz and Driscoll 2008; Jellinek et al. 2014; Reading and Jofré 2015; Haby and Brandle 2018; Kay et al. 2018; Pulsford et al. 2018). Agricultural practices differ across the globe, including the major types of agriculture (Connor 2023), the level of mechanization and intensification (Waha et al. 2020; Daum 2023), and pesticide use (Sharma et al. 2019). These differences could result in varying impacts on snake abundance in different regions.

We quantified the impact of agriculture in the landscape on snake abundance and size in wetlands in the Gatineau/Ottawa area, Canada. A recent study by Gigeroff and Blouin-Demers (2023) documented the effects of landscape composition on snake abundance and size in the same region, but the focal sites were old fields, a human-made habitat, and the focus was on the effects of roads. Here, we wanted to extend on this work (1) with sites selected specifically for variation in the amount of agriculture in the surrounding landscape and (2) by using wetlands as the focal sites, a natural habitat.

We estimated the abundance of garter snakes (*Thamnophis sirtalis*; (Linnaeus, 1758)) and redbelly snakes (*Storeria occipitomaculata* Storer, 1839) in wetlands embedded in landscapes across a gradient from natural to agricultural. We expected higher abundance in wetlands surrounded by more natural habitats compared to agricultural land. We also expected snakes to be smaller on average in agricultural landscapes as a result of increased mortality or access to fewer resources.

Materials and methods

Study site and species

Garter snakes (*Thamnophis sirtalis*) and redbelly snakes (*Storeria occipitomaculata*) are both widely distributed and locally abundant in Ontario and Québec (Carpenter 1952; Wright and Wright 1994; Halliday and Blouin-Demers 2018) and both species occupy wetlands (Carpenter 1952; Wright and Wright 1994; Halliday and Blouin-Demers 2018). We identified >50 potential wetlands (Fig. 1) by inspecting maps in ArcGIS with the Ontario Land Cover Compilation v2.0 (OLCC; OMNRF 2016) and the Comptes des Terres du Québec (CTQ; Québec Institute of Statistics 2019). We then selected study sites after on-the-ground visits, based on permission and accessibility, and whether they were sufficiently open (not closed canopy) and had enough dry ground (not waterlogged or saturated) to place a minimum of 10 cover boards. We retained 31 study wetlands (Fig. 1) embedded in landscapes along a gradient of agricultural to natural. All sites were at least 1 km apart (mean distance = 36 km, median distance = 39 km) to maintain independence of landscape composition and to prevent snake dispersal between sites.

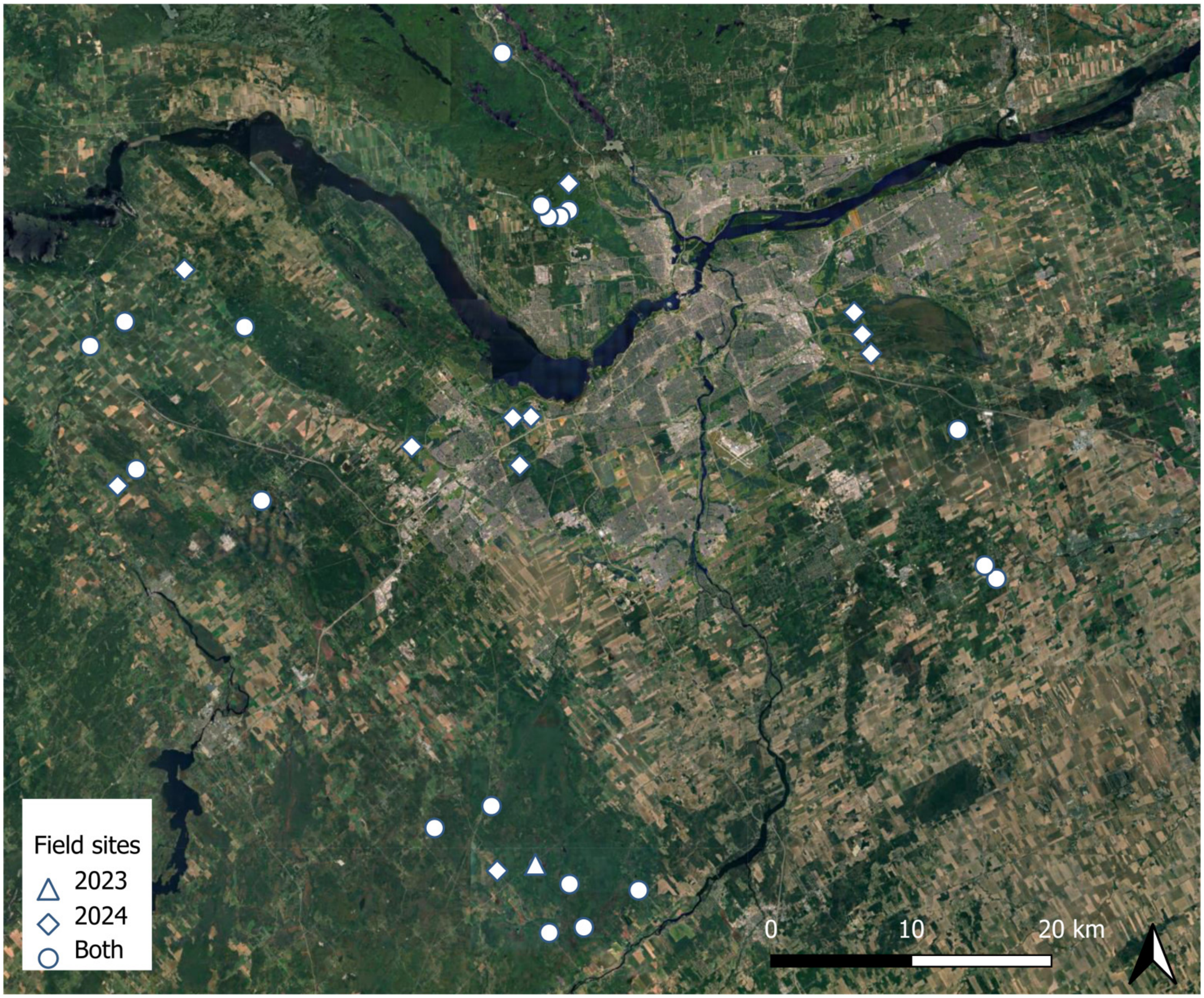
This research was conducted in accordance with Ontario Wildlife Scientific Collector's Authorizations (permit numbers: 1102834, 1105057) and Permis Scientifique du Québec (permit numbers: 23-07-SF-001-GR-3, 24-07-SF-001-GR-0). Ethics approval was granted by the University of Ottawa's Animal Care Committee in accordance with the Canadian Council on Animal Care (protocol number: BLf-4108).

Landscape variables

We quantified the land cover around each wetland within 100 m buffer increments, from 100 to 1000 m (distances commonly used in studies of small vertebrates; Jackson and Fahrig 2015). Buffers were centered on the sampling transect at each site. This was done to determine at what spatial scale the surrounding landscape composition had the greatest effect (i.e., the scale of maximum effect; SI Table 1). Garter snakes and redbelly snakes typically travel well under 500 m (Pisani and Busby 2011; Most 2013), and have relatively small home ranges; up to 500 m^2 for garter snakes and likely smaller for redbelly snakes (Charland and Gregory 1995; Wiens 2008). 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 to 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 saurita* (Linnaeus, 1766), formerly *Thamnophis sauritus* (Linnaeus, 1766) (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 maximum effect of most landscape variables for snake abundance for a similar study to fall within this range, suggesting this is an appropriate scale.

Land cover types were initially classified using the OLCC and CTQ during site selection; however, to confirm land cover classification, we later used the Agriculture and Agri-Food Canada Annual Crop inventory 2021 (AAFC 2021; Supplementary Information; SI Table 2). We grouped land cover classes from 29 classes from OLCC, 9 from CTQ, and 61 categories

Fig. 1. Map of the field sites within the Ottawa/Gatineau area in Eastern Ontario and Southern Quebec, Canada. Diamonds represent sites that were visited only in 2024, triangles represent sites that were only visited in 2023, and circles represent sites that were visited both years. A total of 31 sites were surveyed across a gradient of agricultural landscapes from May to September. The map was created in ArcGis using NAD83 projection system and UTM (zone 18) coordinate system. World imagery base map provided by Esri and collaborators (2009).



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from the AAFC crop inventory into five categories: agriculture, forest, grassland/field, wetland, urban/developed, and open water (see Supplementary Information: SI Table 2). We 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. We used road data from Statistics Canada 2024 Road Network to get road density (km road/km^2 area; Statistics Canada 2024). Land cover types were verified using aerial imagery (City of Ottawa and National Capital Commission 2017) and some ground-truthing. We measured habitat heterogeneity using Shannon diversity index for land covers post hoc and tested it in the models; however, the variable was correlated with land cover variables and was not retained in the models. A binary variable of whether sites were connected to other natural habitat types was also tested post hoc; however, it was also correlated with land cover variables and not retained in the models.

Snake abundance

We used plywood cover boards (60 × 60 × 1.27 cm) to attract snakes by providing a warm hiding place (Halliday and Blouin-Demers 2015). Over the snakes' active seasons of 2023 and 2024, we placed boards along transects varying between 100 and 200 m (depending on the size of the wetland), every 10 m. We 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 08:00 and 18:00 on clear days when the air tempera-

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ture was between 10 and 30 °C. The majority of snakes (91% of garter, 99% of redbelly) were captured under the cover boards. We measured snakes from the tip of the snout to the end of the cloacal opening (snout-vent length; SVL), sexed them with cloacal probes, and uniquely marked them on the ventral scales anterior to the cloaca with a medical cautery unit, following Winne et al. (2006). We classified individuals that were too small to probe or accurately determine 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), so we used the number of unique individual snakes captured as a proxy for abundance instead (Gigeroff and Blouin-Demers 2023).

Statistical analyses

We modelled the relationship between agriculture, snake abundance, and snake size (SVL) using generalized linear mixed-effect models (GLMMs). The models included other land cover types and temporal variables that could influence snake abundance (and/or the probability of finding a snake), like day of year, time of day, and temperature as covariates. The modelling was done in R (R Core Team 2021; R version 4.3.2). We calculated Moran's I to assess spatial autocorrelation; this analysis provided no evidence of autocorrelation (Supplementary Information: SI Table 3). The response variable was the total number of snakes captured at a site for each survey, over two field seasons for abundance models, and included an offset variable for the number of cover boards checked at each site to account for sampling effort. We included a quadratic term for day of year since abundance is not expected to increase linearly throughout the season. We expected 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. Inspection of pairwise correlation coefficients and variance inflation factors (VIFs; using the car package in R; Fox and Weisberg 2019) 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; Supplementary Information; SI Table 4) and its inclusion improved model fit and explanatory power. For SVL models, however, the polynomial day of year terms showed extremely high pairwise correlation and collinearity (Pearson's $r > 0.9$ and VIFs > 150), well above the common VIF cut-off threshold of 5 or 10 (Marcoulides and Raykov 2019), indicating that both variables were explaining the same variation in the data. Because the quadratic day of year term was redundant and causing correlation and collinearity issues, we removed it from the SVL models. We modelled abundance using GLMMs with a negative binomial distribution, since there was overdispersion, and a log link function to ensure positive values. This was done using packages lme4 and lmerTest (Bates et al. 2015; Kuznetsova et al. 2017). For SVL, we fit linear mixed-effects models using the package nlme (Pinheiro et al. 2025). Neonates and unsexed snakes were removed from the analyses to avoid potentially confounding mean snake size with greater or fewer neonates in the population. Neonates were identified based on mean adult garter and redbelly snake sizes. Snakes that were too small to sex accurately were also removed from the dataset. We 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, we fit site as a random effect for all models. We fit year as a categorical fixed effect because it falls below the suggested limit of >5 levels for a random effect (Bolker et al. 2009; Oberpriller et al. 2022). We assessed model fit and confirmed that model assumptions were met through diagnostic plots, including DHARMa plots (Hartig et al. 2024).

To determine which land covers to include in the model, we plotted the percentage of each land cover across sites to determine whether sites varied appreciably for each land cover (see Supplementary Information; SI Fig. 1 for land cover percentages and Fig. 2 for modelling decision flow chart). The percentage of open water, grassland, and road density in the landscape showed little variation across sites (Supplementary Information; SI Fig. 1), so they were not included in the model to avoid over-parameterization. This resulted in the inclusion of crop, pasture, forest, urban, and wetland covers. However, for some models, forest and crop cover were correlated, resulting in the removal of forest cover (see modelling decision flow chart; Fig. 2).

The scale of maximum effect for each land cover variable was determined by taking the Pearson's correlation coefficient between abundance and the land covers at each buffer size, and likewise for SVL (Supplementary Information: SI Table 1). To check for correlation and collinearity among all variables, we assessed the correlation matrices for each model's set of variables and calculated VIFs (Supplementary Information; SI Table 4). If pairs of variables were strongly correlated, one was removed from the model (Fig. 2).

We centered and scaled variables for the abundance models, given the differing scales of measurement for the variables. Reduced models were compared via LRT, corrected Akaike's information criterion, and coefficient of determination (R^2) to confirm that dropping non-significant terms did not affect model performance. We also used LRTs for null hypothesis testing to compare the explanatory power of percent agriculture in the models.

Results

Snake abundance and size

Across all sites, we 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 (37% female, 30% male, and 33% unsexed), but was skewed towards unsexed for redbelly snakes (26% females, 19% males, and 54% unsexed) due to the difficulty of sexing small snakes. Unsexed snakes were excluded from the SVL models. Garter snakes ranged in size from 13 to 70 cm SVL, while redbelly snakes ranged in size from 6 to 29 cm SVL (Fig. 3).

 Can. J. Zool. **104:** 1–12 (2026) | dx.doi.org/10.1139/cjz-2025-0120

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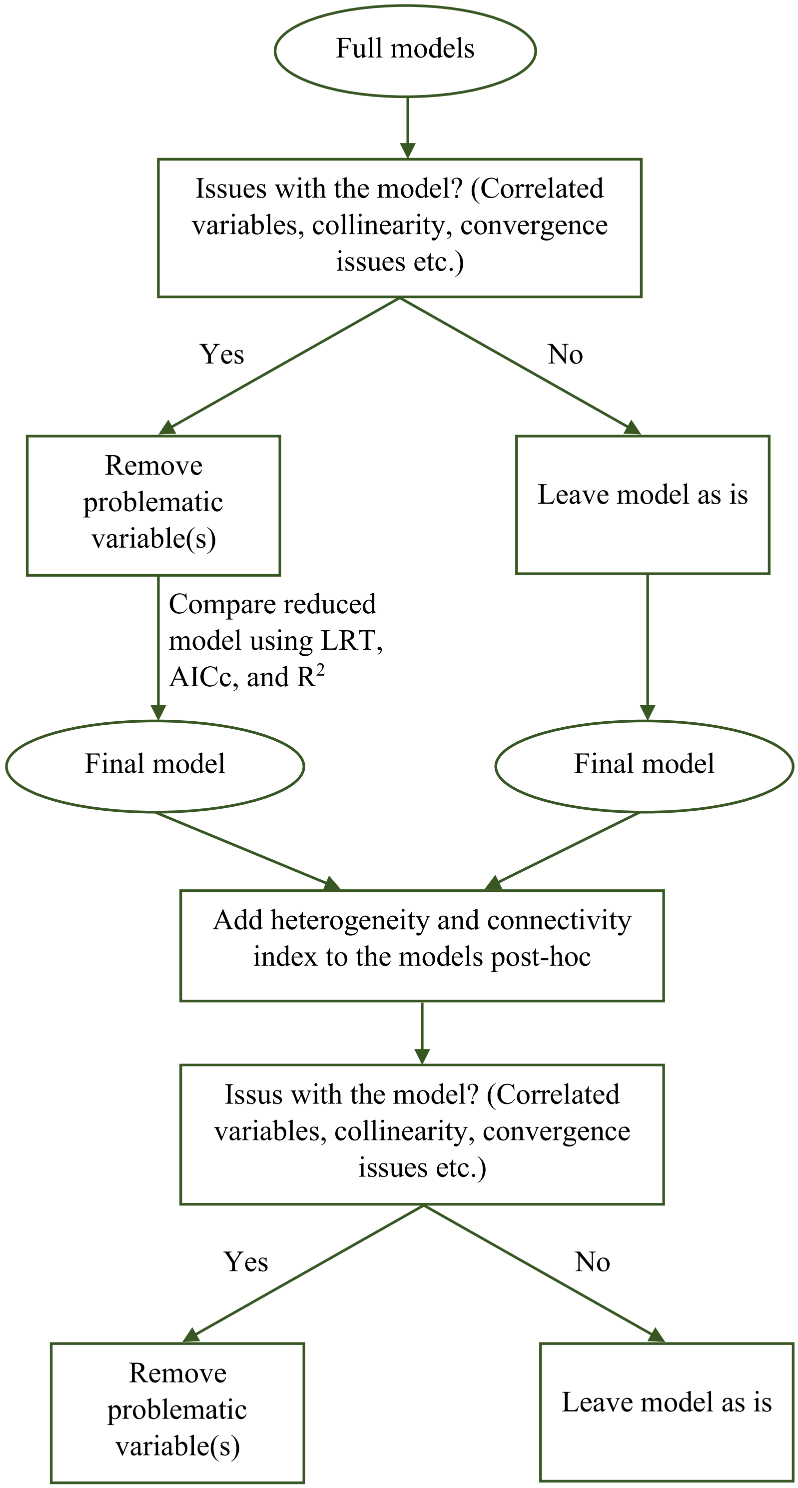
Fig. 2. Decision-making flow chart depicting the modelling process.

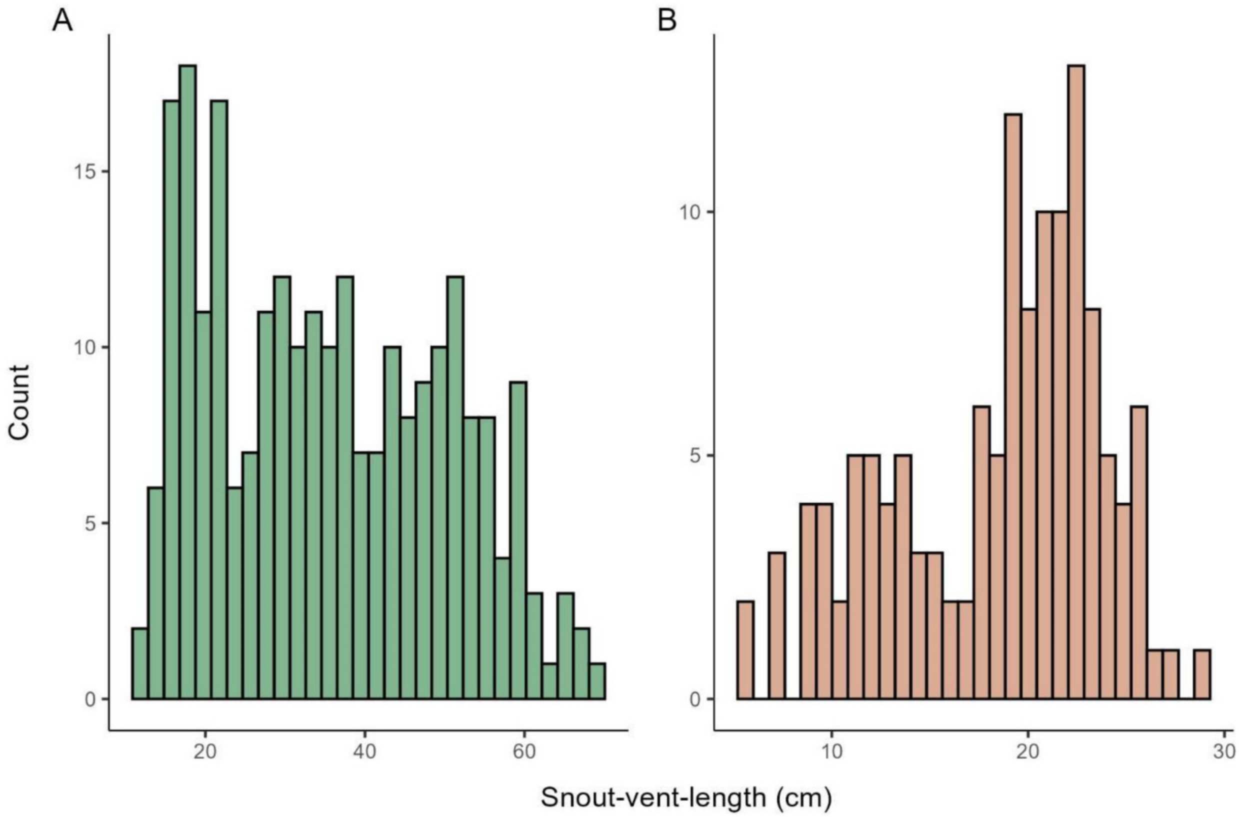


Predictors of garter snake abundance

The scale of maximum effect of landscape variables ranged from 400 to 1000 m for garter snake abundance (Supplementary Information: SI 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, to maintain site independence, 1000 m was kept as the maximum buffer size. Because the correlation coefficient did not vary greatly across buffer sizes for each land cover (Supplementary Information; SI Figs. 2 and 3), and given the small typical distances snakes travel (Pisani and Busby 2011; Most 2013), a 1000 m buffer size is likely sufficient.

The final model for garter snake abundance included percent crop (1000 m), pasture (900 m), wetland (1000 m), and

Fig. 3. Histograms depicting the frequency and spread of snake size, given by snout-vent-length (SVL; cm) for (A) garter snakes (*Thamnophis sirtalis*) (green), and for (B) redbelly snakes (*Storeria occipitomaculata*) (red). Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in the Gatineau/Ottawa area, Ontario/Quebec, Canada from May to September 2023–2024.



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urban (700 m) land covers, day of year, day of year^2, time of day, and temperature as predictors (Table 1). Significant predictors of garter snake abundance under the final model were day of year, day of year^2, time of day, and percent wetland cover. Snake abundance slightly declined throughout the season and then increased later in the summer, and were found more frequently later in the day. More snakes were found at sites with more wetland land cover (1000 m) in the surrounding landscape (Table 1). Percent crop (1000 m) was not a significant predictor of garter snake abundance under a 95% significance level (i.e., alpha = 0.05); however, under a 85% significance level (alpha = 0.15), it was significant. Fewer garter snakes were found in wetlands with increasing crop cover in the landscape, suggesting 18% fewer snakes per 10% increase in crop cover in the landscape (95% CI [−34, 3], $p = 0.09$; Fig. 4). Urban land cover was also significant at the 90% confidence level, expecting fewer snakes with increasing urban land cover (700 m) in the surrounding landscape. There was no significant difference in snake abundance with increasing pasture cover (900 m; Table 1).

Predictors of redbelly snake abundance

The scale of maximum effect of landscape variables for redbelly snake abundance ranged from 100 to 1000 m (Supplementary Information: SI Table 1). The final model included percent crop (300 m), pasture (900 m), wetland (1000 m), and urban (100 m) land covers, day of year, day of year^2, time of day, and temperature (Table 1). Time of day, day of year, and wetland cover (1000 m) were significant predictors, with more snakes being found later in the day, later in the season, and at sites with more wetland cover in the landscape (Table 1). There was no significant difference in the abundance of redbelly snakes in wetlands with increasing cropland (300 m) in the surrounding landscape; however, the effect size was larger, with the model predicting 34% fewer redbelly snakes per 10% increase in crop cover (95% CI [−68, 36], $p = 0.26$; Fig. 4). There was no significant difference in redbelly snake abundance as a function of pasture cover (900 m).

Predictors of garter snake size

The scale of maximum effect of landscape variables for garter snake size ranged from 200 to 1000 m (Supplementary Information: SI Table 1). The final model for garter snake size included percent crop (800 m), pasture (900 m), wetland (300 m), and urban (1000 m) land covers, sex, day of year, time of day, and temperature as predictors (Table 2). Sex was a significant predictor, and time of day was significant at the 90% confidence level (alpha = 0.10), expecting male snakes to be smaller than females, and expecting to see more small snakes later in the day (Table 2). Garter snakes did not differ significantly in size across sites

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Table 1. Summary statistics for the final selected generalized linear mixed models for garter snake (*Thamnophis sirtalis*) and redbelly snake (*Storeria occipitomaculata*) abundance.

Parameter	Estimate	Standard error	*z*-value	*p*-value	
Model: garter snake abundance					
(Intercept)	– 3.83	0.18	– 21.52	< 0.01	***
Crop (1000 m)	– 0.26	0.17	– 1.53	0.13	
Pasture (900 m)	– 0.07	0.16	– 0.42	0.68	
Wetland (1000 m)	0.32	0.15	2.15	0.03	*
Urban (700 m)	– 0.30	0.16	– 1.88	0.06	.
Day of year	– 0.17	0.09	– 1.96	0.05	*
Day of year^2	– 0.30	0.09	– 3.18	< 0.01	**
Time of day	0.56	0.09	6.11	< 0.01	***
Temperature	– 0.13	0.10	– 1.41	0.16	
Model: redbelly snake abundance					
(Intercept)	– 3.83	0.18	– 21.52	<0.01	***
Crop (300 m)	– 0.26	0.17	– 1.53	0.13	
Pasture (900 m)	– 0.07	0.16	– 0.42	0.68	
Wetland (1000 m)	0.32	0.15	2.15	0.03	*
Urban (100 m)	– 0.30	0.16	– 1.88	0.06	.
Day of year	– 0.17	0.09	– 1.96	0.05	*
Day of year^2	– 0.30	0.09	– 3.18	<0.01	*
Time of day	0.56	0.09	6.11	<0.01	***
Temperature	– 0.13	0.10	– 1.41	0.16	

Note: Snake abundance was surveyed at 31 sites over an agricultural gradient in the Gatineau/Ottawa area from May to September 2023–2024. Parameter estimates are on a log scale and were centred and scaled. indicates nearly significant at alpha = 0.05 for p values of 0.05 < p <= 0.1, $*$ indicates significance at alpha = 0.05 for p values of 0.01 < p <= 0.05, $**$ indicates significance at alpha = 0.05 for p values of 0.01 < p <= 0.001, $***$ indicates significance at alpha = 0.05 for p values of p < 0.001. The superscript for day of year is an exponent of 2 (this is a polynomial variable; day of year and day of year squared.

with increasing crop or pasture cover in the landscape, although the model predicted 1 cm smaller snakes per 10% increase in pasture cover (95% CI [−2.69, 0.71], $p = 0.24$; Fig. 5).

Predictors of redbelly snake size

The scale of maximum effect of landscape variables for redbelly snake size ranged from 100 to 1000 m (Supplementary Information: SI Table 1). The final model for redbelly snake SVL included percent crop (800 m), pasture (800 m), wetland (1000 m), and urban (300 m) land covers, day of year, time of day, sex, temperature, and vegetation cover as predictors (Table 2). Sex was the only significant predictor of redbelly snake size at the 95% confidence level, with male snakes being smaller than females (Table 2). At a 90% confidence level, the effect of crop cover (800 m) was significant and redbelly snakes were predicted to be 0.4 cm larger per 10% increase in crop cover (95% CI [−0.1, 0.9], $p = 0.08$; Fig. 5). A 24% increase in crop cover would be required to see a 1 cm difference in snake size. For pasture cover (800 m), the model predicted 0.4 cm smaller snakes per 10% pasture cover increase (95% CI [−1, 0.2], $p = 0.15$), requiring a 24% increase in pasture cover to see a 1 cm difference in snake size.

Discussion

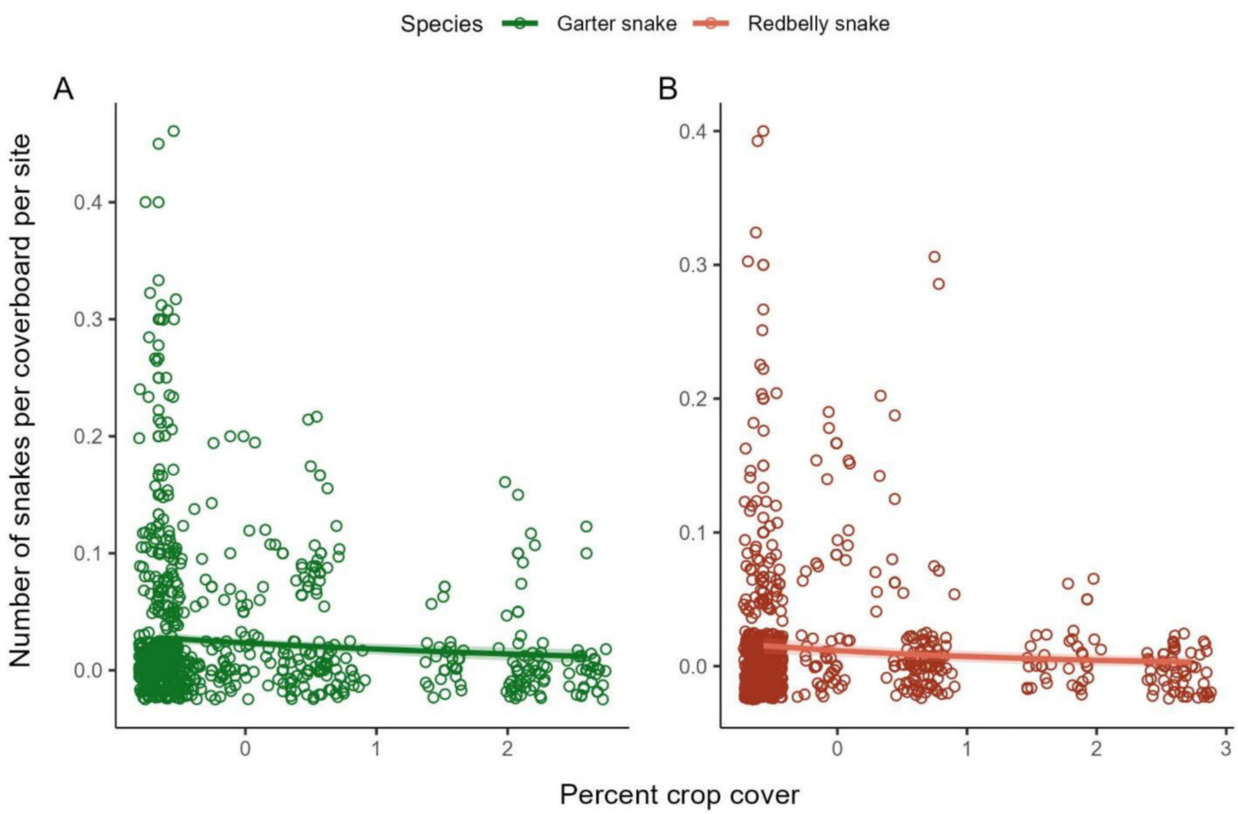
Landscape effect of agriculture on garter and redbelly snakes

Snake abundance in wetlands may decline with increasing surrounding agricultural land cover. While these results were not always significant, the effects were strong and always negative. The negative effect of agriculture in the landscape is likely more complex than just how much is present in the surrounding area.

Garter snake size did not differ across the agricultural gradient; however, redbelly snakes were predicted to be slightly larger in landscapes with more crop cover. The effect size for expected size differences with increasing crop cover in the landscape was, however, not biologically significant, requiring a minimum of a 24% increase in crop cover just to see a 1 cm difference in snake size. This suggests that more cropland in the landscape may not greatly restrict access to resources or cause higher mortality such that individuals are unable to reach larger sizes.

Several previous studies found neutral or nonsignificant effects of agriculture on reptile abundance or presence (Schutz and Driscoll 2008; Jellinek et al. 2014; Suazo-Ortuño et al. 2015; Pulsford et al. 2018). Pulsford et al. (2018) looked at the response of frogs and lizards, which likely differ in habitat

Fig. 4. Model-predicted garter snake (*Thamnophis sirtalis*) abundance (A) and redbelly snake (*Storeria occipitomaculata*) abunda1nce (B) versus the percentage of crop cover in the landscape. Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in the Gatineau/Ottawa area, Ontario/Quebec, Canada from May to September 2023–2024 to determine the effect that agriculture has on snake abundance. Trend lines were predicted from the final generalized linear mixed effects models. The model predictions are given as the number of snakes per site, setting the number of coverboards to oneto make predictions consistent across sites and to account for the varying number of boards at each site. The response variable is given as the predicted number of snakes that would be found under a single board at each site, per survey.



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needs and dispersal from snakes. Pulsford et al. (2018) and Suazo-Ortuño et al. (2015) looked specifically at the effects of grazing on a local scale, which we also found to have a more neutral effect, but at the landscape scale. The scale at which the effects of agriculture are examined is important. Haby et al. (2018) 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 for abundance. The effect of agriculture may be stronger at a local scale (Wasiolka and Blaum 2011; Reading and Jofré 2015; Guiller et al. 2022), where habitats tend to be directly replaced, compared to the surrounding landscape, where natural habitats can remain.

Agriculture and habitat heterogeneity

Wetlands in agricultural landscapes may no longer support populations if agriculture in the surrounding landscape becomes too dominant. We attempted to examine the influence of habitat heterogeneity on snake abundance and size in this study post-hoc; however, the heterogeneity index variable was correlated with landcover variables, and therefore had to be removed from models, thus our interpretation is speculative. 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 and Weatherhead 2001, 2002; Wisler et al. 2008; DeGregorio 2011), 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. They 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 persist in homogeneous agricul-

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Table 2. Summary statistics for the final selected linear mixed models for garter snake (*Thamnophis sirtalis*) and redbelly snake (*Storeria occipitomaculata*) size (snout-vent-length; SVL).

Parameter	Estimate	Standard error	DF	*t*-value	*p*-value	
Model: garter snake SVL						
(Intercept)	48.64	7.31	140	6.65	<0.01	***
Crop (8000 m)	0.07	0.08	21	0.91	0.38	
Pasture (900 m)	– 0.10	0.08	21	– 1.22	0.24	
Wetland (300 m)	0.05	0.06	21	0.73	0.47	
Urban (1000 m)	– 0.16	0.22	21	– 0.73	0.47	
Day of year	0.01	0.02	140	0.62	0.53	
Temperature (C)	– 0.20	0.24	140	– 0.83	0.41	
Time of day	– 0.02	0.35	140	– 0.06	0.95	
Sex (male)	– 7.58	1.56	140	– 4.85	<0.01	***
Model: redbelly snake SVL						
(Intercept)	20.79	2.27	41	9.15	<0.01	***
Crop (800 m)	0.04	0.02	11	1.89	0.08	.
Pasture (800 m)	– 0.04	0.03	11	– 1.55	0.15	
Wetland (1000 m)	0.00	0.02	11	0.17	0.87	
Urban (300 m)	– 0.06	0.04	11	– 1.56	0.15	
Day of year	0.01	0.01	41	1.33	0.19	
Temperature (C)	0.03	0.06	41	0.54	0.59	
Time of day	0.08	0.10	41	0.84	0.41	
Sex (male)	– 1.52	0.44	41	– 3.50	<0.01	**

Note: Snakes were sampled at 31 sites over an agricultural gradient in the Gatineau/Ottawa area from May to September 2023–2024. indicates nearly significant at alpha = 0.05 for p values of 0.05 < p <= 0.1, * indicates significance at alpha = 0.05 for p values of 0.01 < p <= 0.05, ** indicates significance at alpha = 0.05 for p values of 0.01 < p <= 0.001, *** indicates significance at alpha = 0.05 for p values of p < 0.001.

tural landscapes. This is likely also influenced by factors like the type of agriculture or the kind of land management, and can therefore alter the impact of agriculture on snake populations.

Limitations and future directions

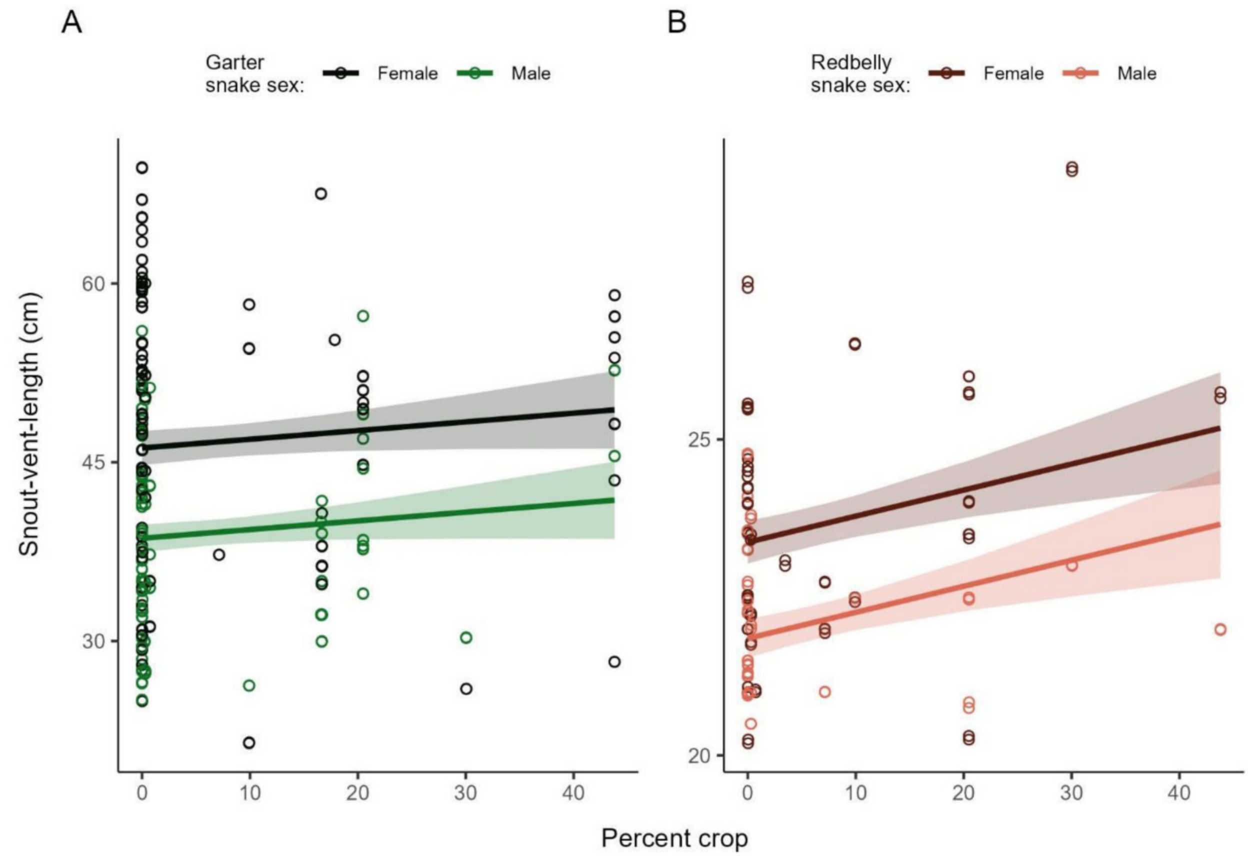
A stronger effect of agriculture on a landscape scale may have been found with a larger sample size or with sites surrounded completely by agriculture. The highest percentage of agricultural land cover was around 80% in our study. Given that the scale of maximum effect for several land cover variables 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. Given that the correlation coefficient varied very little over the range of buffer sizes (Supplementary Information: SI Figs 2 and 3), however, 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, 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 tend to have less natural land cover surrounding it; however, the proximity to other natural land covers could affect how easily snakes are able to access them. While some studies found no effect of patch configuration or connectivity (Schutz and Driscoll 2008; Jellinek et al. 2014), this could be taxon-dependent. Other studies have found that snakes generally avoid using or travelling through agriculture (Row et al. 2012; Marshall et al. 2020), which suggests that lower connectivity could have an effect.

Implications of increasing agriculture

This research has potential implications for land management practices. For instance, our results can influence 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 (Simberloff and Abele 1982; Fahrig 2013). It may be possible to offset the negative effects of agriculture on snakes as long as there are other land covers and habitats that remain accessible. The availability and quality of microhabitats within agricultural landscapes 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

Fig. 5. Model-predicted snake size (snout-vent-length; SVL) for garter snakes (*Thamnophis sirtalis*) (A) and redbelly snake (*Storeria occipitomaculata*) (B) versus the percentage of crop cover in the landscape. Snakes were sampled at 31 wetland sites across a gradient of agricultural landscapes in the Gatineau/Ottawa area, Ontario/Quebec, Canada from May to September 2023–2024 to determine the effect that agriculture has on snake abundance. Trend lines were predicted from the final linear models.



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done to disentangle the mechanisms through which agriculture negatively affects snakes.

Acknowledgements

We are grateful to Lenore Fahrig and to Julie Lee-Yaw for their valuable input on previous drafts of this manuscript. We are thankful to our assistants, Hannah Meikle and Jonathan Tran, for their hard work in the field. We thank the landowners who graciously allowed us to use their property.

Article information

History dates
Received: 10 September 2025
Accepted: 19 March 2026
Accepted manuscript online: 20 May 2026
Version of record online: 19 June 2026

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Data availability
Data generated and analyzed during this study are available on the GitHub repository at https://github.com/Michelle-49/agriculture-snake-abundance.

Author information

Author ORCIDs
Michelle L. LaFlamme https://orcid.org/0009-0003-3936-5621

Author contributions
Conceptualization: MLL, GB
Data curation: MLL
Formal analysis: MLL
Funding acquisition: MLL, GB
Investigation: MLL
Methodology: MLL
Project administration: MLL, GB
Resources: GB
Software: MLL
Supervision: GB
Validation: MLL
Visualization: MLL

Writing – original draft: MLL
Writing – review & editing: MLL, GB

Competing interests

Authors declare no competing interests.

Funding information

This research was funded by an NSERC (Natural Sciences and Engineering Research Council of Canada) Discovery Grant to Gabriel Blouin-Demers (grant number: RGPIN-2024-03896) and graduate scholarships from NSERC and the Ontario Graduate Scholarship to Michelle LaFlamme.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2025-0120.

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