Habitat selection by Common Gartersnakes (*Thamnophis sirtalis*) is affected by vegetation structure but not by location of Northern Leopard Frog (*Lithobates pipiens*) prey

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Abstract

Understanding the factors affecting habitat selection of species is important for effective management and for conservation because habitat selection affects fitness. We tested the competing, but not mutually exclusive, hypotheses that habitat selection of Common Gartersnakes (*Thamnophis sirtalis*) at a fine spatial scale is driven by vegetation structure or by Northern Leopard Frog (*Lithobates pipiens*) prey abundance. We conducted surveys for snakes and frogs in six, 1-ha study grids in eastern Ontario in 2014 and 2015. Common Gartersnakes used areas dominated by forbs more than expected based on availability, and used grassy areas less than expected based on availability. Gartersnakes showed no preference for sites with more frogs. Thus, vegetation structure is important in habitat selection of Common Gartersnakes, but Northern Leopard Frog abundance is not. Common Gartersnakes and Northern Leopard Frogs did have a preference for forbs, but gartersnakes do not appear to be using habitat specifically based on frog abundance at a fine scale. Future work should study habitat use by snakes over a longer period to account for high variability in frog abundance and for temporal changes in habitat structure. Future work should also examine the distribution of other prey items in relation to the distribution of snakes.

Key words: Common Gartersnake; *Thamnophis sirtalis*; Northern Leopard Frog; *Lithobates pipiens*; eastern Ontario; habitat selection; habitat structure; prey; predator; wetland

Introduction

Habitat selection by animals is important because it affects their fitness (Fretwell and Lucas 1969; Rosenzweig 1981; Morris 1988, 2003a). Individuals should make adaptive habitat selection decisions to maximize their fitness (Morris 2011). Identifying which resources are most important to a species can be a crucial step in not only understanding habitat selection and fitness, but also in the management and conservation of a species (Morris 2003a,b, 2011). Habitat selection can be defined as "the process whereby individuals preferentially use, or occupy, a non-random set of available habitats" (Morris 2003a: 2). In this study, we examined habitat selection by snakes in relation to vegetation characteristics, water levels, and amphibian abundance in wetlands near Ottawa, Ontario, Canada. The only snake species that we encountered in sufficient numbers for statistical analyses was Common Gartersnake (*Thamnophis sirtalis*), therefore our study focusses on this species.

Although *T. sirtalis* have been studied for decades, few studies have explicitly examined their habitat preferences. Nevertheless, some of the variation across their range has been described by Ernst and Ernst (2003). Carpenter (1952) found that over 70% of *T. sirtalis* encountered were in grassy habitats, with most of the remainder associated with wetlands. Fitch (1965) found that *T. sirtalis* preferred relatively open habitats, including pond margins, meadows, fields, and edges of woodlands. Hart (1979) found *T. sirtalis* more in marsh habitat than pond habitat, and typically in areas with low moisture content. Charland and Gregory (1995) found that *T. sirtalis* showed a strong preference for areas with more overhead cover, and avoided open water, but also found that gravid females preferred warmer, rocky habitats. Burger *et al.* (2004) found that *T. sirtalis* in a riparian habitat showed a preference for basking in open areas on the ground rather than on branches or logs. Gregory (1984) found that *T. sirtalis* in coastal British Columbia were only found at sites that were dominated by freshwater rather than saltwater. Our work with *T. sirtalis* in eastern Ontario and western Quebec (Halliday and Blouin-Demers 2015, 2016, 2017; Halliday *et al.* 2015) demonstrated a density-independent preference for field over forest habitat, likely because fields have more optimal temperatures than forests, which lead to higher fitness (Halliday and Blouin-Demers 2016).

We conducted this study partly because eastern Ontario is a part of the range of *T. sirtalis* that is underrepresented in the literature. Studying habitat use by free-ranging *T. sirtalis* in open habitats expands on our previous work studying habitat selection between field

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and forest habitats in large enclosures (Halliday and Blouin-Demers 2015, 2016; Halliday *et al.* 2015). Our main goal was to test two competing, but not mutually exclusive, hypotheses: (1) habitat selection by gartersnakes is driven by frog abundance and (2) habitat selection by gartersnakes is driven by the need to thermoregulate. More specifically, we first wanted to determine if habitat use by *T. sirtalis* was related to frog abundance in different habitats and we predicted that gartersnakes should be more abundant where frogs are more abundant. Food is often considered a very important aspect of habitat quality (Kennedy and Gray 1993), but this might not be the case for snakes because most eat large meals infrequently (Shine 1986). Yet some studies with snakes have suggested that habitat use may be driven by food abundance (Robertson and Weatherhead 1992). Habitat quality for snakes is often linked to structural characteristics of habitats that allow them to thermoregulate or to hide (Blouin-Demers and Weatherhead 2001; Halliday and Blouin-Demers 2015, 2016). Therefore, we also wanted to determine if habitat use by *T. sirtalis* was related to structural characteristics of the different habitats, and we predicted that gartersnakes should be more abundant in more open habitats because these have higher thermal quality in temperate regions (Blouin-Demers and Weatherhead 2001; Row and Blouin-Demers 2006; Halliday and Blouin-Demers 2016).

Methods

Study site and data collection

In June 2014, we set up six study grids in the Stony Swamp sector of the National Capital Greenbelt in Ottawa, Ontario (45.283°N, 75.817°W; Figure 1). Vegetation characteristics were variable both among and within grids, varying from cattail (*Typha* sp.) dominated to mixes of shrub, grass, and forb. Each study grid was 100 × 100 m and we separated each grid into 25, 10 × 10 m sectors, marking the corners of each sector with bamboo poles marked with flagging tape. We placed a 60 × 60 cm cover object in the centre of each sector on substrate without standing water. In general, cover objects are a useful tool to monitor snakes (Halliday and Blouin-Demers 2015; Retamal Diaz and Blouin-Demers 2017). Cover objects were made of either tin (12 of 25 sectors) or plywood (13 of 25 sectors), which have been shown to be equally effective to sample small snakes in our area (Retamal Diaz and Blouin-Demers 2017).

We monitored each grid up to six times per year, but no more than once per week, between June and August of 2014 and 2015. More specifically, we visited grids 1 and 2 six times, grid 6 eight times, grids 3 and 5 nine times, and grid 4 ten times. When monitoring a grid, three to four people walked back and forth across the grid with an even spacing (~2 m between individuals) and at a constant pace. While searching for snakes and frogs, we looked under each cover object once during each survey, carefully looked in and around natural cover objects such as coarse woody debris without disturbing the habitat, and looked in the dense vegetation. When we detected a snake (either under a cover object or in the open), we worked together to capture the snake by hand. After catching each snake, we marked its ventral scales with a unique code using a medical cautery unit (see method and rationale in Winne *et al*. 2006). We also determined the sex of each snake and measured its snout-vent length and mass. We recorded which grid and sector the snake was caught in and released each snake at its point of capture. While monitoring each grid, we also counted the number of frogs (identified to species) encountered in each sector of each grid as a metric of food abundance; frogs are one of the main food sources for *T. sirtalis* (reviewed in Halliday 2016).

We characterized the habitat features in each sector of each grid based on the dominant vegetation class (cattail, dominant tree species, fern, forb, grass, horsetail, shrub), maximum height of vegetation, percent of sector covered by standing water, and maximum depth of water in the sector. We recorded up to two dominant vegetation classes in each sector if the vegetation was mixed.

Analyses

We tallied the number of snakes and frogs of each species encountered in each sector of each grid during each year of our study. For snakes, this tally is the number of individuals in each sector, while for frogs this tally is the number of frogs detected in each sector. We only had one recapture of a snake in the same sector, and we only counted that individual once within that sector. We encountered Common Gartersnake, Northern Watersnake (*Nerodia sipedon*), Red-bellied Snake (*Storeria occipitomaculata*), Eastern Milksnake (*Lampropeltis triangulum*), Green Frog (*Lithobates clamitans*), Northern Leopard Frog (*Lithobates pipiens*), Spring Peepers (*Pseudacris crucifer*), and a juvenile Eastern Newt (*Notophthalmus viridescens*); however, we encountered only enough *T. sirtalis* and *L. pipiens* for statistical analysis (Table 1). Despite our large array of cover objects, we only caught two *T. sirtalis* under covers, although we did catch all *S. occipitomaculata* and all *L. triangulum* under the covers.

We pooled *T. sirtalis* and *L. pipiens* abundances across surveys and converted each into a binary presence/absence variable of a species in each sector of each grid during each year. We then analyzed the presence/absence of *T. sirtalis* and *L. pipiens* within a sector using general linear mixed effects models with a binomial distribution in R (package lme4; function glmer; Bates *et al.* 2015). We built models with different combinations of the following fixed effects: presence/absence of each vegetation class, vegetation height, percent water, water depth, presence/absence of *L. pipiens* (only for the analysis of *T. sirtalis*), and year. We used grid ID as a random effect in all models. We compared models with different fixed effects using Akaike Information

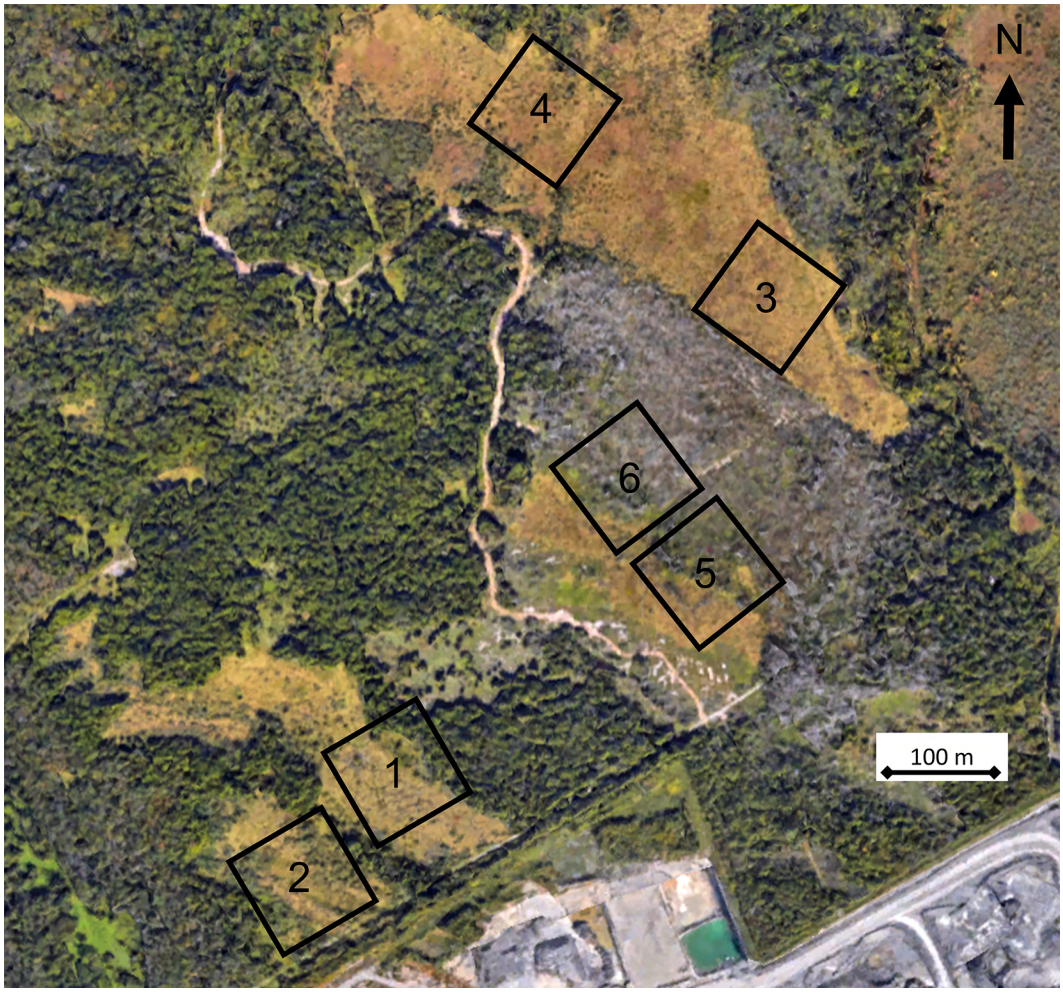

FIGURE 1. Layout of grids at study site in eastern Ontario, Canada. Map data © Google Canada.

TABLE 1. Abundance of snakes and amphibians encountered (number of unique individuals for snakes, but not necessarily for amphibians) in each year of a habitat selection study in six, 1-ha study grids near Ottawa, Ontario in 2014 and 2015.

Scientific name	Common name	2014	2015
Lampropeltis triangulum	Eastern Milksnake	1	1
Nerodia sipedon	Northern Watersnake	2	1
Storeria occipitomaculata	Red-bellied Snake	9	2
Thamnophis sirtalis	Common Gartersnake	20	36
Lithobates clamitans	Green Frog	7	4
Lithobates pipiens	Northern Leopard Frog	142	18
Notophthalmus viridescens	Eastern Newt	1	0
Pseudacris crucifers	Spring Peeper	3	7

Criterion (AIC; package stats; function AIC; R Core Team 2016) and selected the model with the lowest AIC as the final model; we considered models within 2 AIC units of the best model to be competing models and used model averaging to determine effect size (Burnham and Anderson 2002). We conducted all analyses in R version 3.3.0 (R Core Team 2016).

We conducted a second analysis of the abundance of both *T. sirtalis* and *L. pipiens* based on the total number of individuals encountered on each grid during each survey. For this analysis, abundance is the number of unique *T. sirtalis* encountered. This is likely also the number of unique *L. pipiens* counted because our unit of replication is a single survey event in a grid where

it is highly unlikely that we would count the same frog twice. We used general linear models with a Poisson distribution (package stats; function glm) with the abundance of *T. sirtalis* or *L. pipiens* as the dependent variable and with year and grid identification as the independent variables. In the analysis of *T. sirtalis*, we also included the abundance of *L. pipiens* as an additional independent variable. We used bias-corrected Akaike Information Criterion (AICc; package qpcR; function AICc; Spiess 2014) to compare models for this analysis due to low sample size.

Finally, we compared the use of different vegetation types by *T. sirtalis* and *L. pipiens* to the availability of those vegetation types based on the methods described in Johnson (1980). We summed the number of captures and observations of each species in each dominant vegetation type during each year, and calculated the proportion of observations in each vegetation type. We then summed the number of sectors across all study grids that contained each dominant vegetation type, and calculated a proportion. We then compared use versus availability data (transformed into percent) for each species in each vegetation type in each year using χ^2 analysis in R (package stats; function chisq.test).

Results

Thamnophis sirtalis was more likely to be encountered in sectors with forbs (log odds ratio: 0.87, $z = 2.04$, $P = 0.04$) and was less likely to be encountered in sectors with grass (log odds ratio = −0.78, $z = 2.04$, $P = 0.04$; Figure 2a, Table S1). The probability of presence of *T. sirtalis* was unaffected by all other vegetation classes. Two of our study grids (5 and 6) had significantly more *T. sirtalis* than the other four grids ($P < 0.01$; Figure 3a, Table S2). These grids had high forb coverage, medium shrub and grass coverage, low fern and cattail coverage, and were rebounding from a 2012 forest fire. *Thamnophis sirtalis* was also more abundant in 2015 than in 2014 ($z = 3.23$, $P < 0.01$). The probability of presence of *T. sirtalis* was unaffected by water coverage or depth or frog abundance. *Thamnophis sirtalis* was more likely to be found in habitats with forbs relative to their availability, and were less likely to be found in habitats with grass relative to their availability in both 2014 ($\chi^2_{12} = 76.06$, $P < 0.01$) and 2015 ($\chi^2_{12} = 44.78$, $P < 0.01$; Figure 1a, Table S3).

Lithobates pipiens was more likely to be encountered in 2014 than in 2015 (log odds ratio = −2.39, $z = 5.23$, $P < 0.01$; Table S4), but their presence was unaffected by all vegetation classes (Figure 2b, Table S4). Two of our study grids (5 and 6) again had significantly more *L. pipiens* than other grids (Figure 3b, Table S5). According to the use-availability analysis, *L. pipiens* used habitats with forbs more than expected based on their availability, and used habitats with shrubs much less than expected based on their availability in both 2014 ($\chi^2_{12} = 55.82$, $P < 0.01$) and 2015 ($\chi^2_{12} = 70.04$, $P < 0.01$; Figure 2b, Table S3).

Discussion

Our study demonstrates that vegetation structure is an important predictor of habitat selection by *T. sirtalis*, but *L. pipiens* abundance is not. These results support our second hypothesis (habitat selection for thermoregulation), but do not support our first hypothesis (habitat selection for food). Our previous work (Halliday and Blouin-Demers 2016) demonstrated the importance of vegetation structure and habitat selection for thermoregulation at a coarse scale, where gartersnakes used warm open field habitat much more than cool forested habitat. In this study, we demonstrate that *T. sirtalis* prefer certain types of open habitats at a finer spatial scale. Specifically, we found more *T. sirtalis* near forbs (i.e., flowering plants like clover and vetch) more than expected based on availability, and fewer in grassy habitat than expected based on availability. Areas with high coverage of forbs were typically quite dry and offered good sites for basking. This forb habitat was also most abundant in sites 5 and 6 and is unique in the area due to a recent forest fire (summer 2012). Sites 5 and 6 had many fallen cedar trees, which provided potential cover where snakes could hide, mixed with plenty of small open sites for basking. We were able to observe snakes under these fallen trees without disturbing the habitat because the trunks were kept elevated from the ground by remaining branches. Although our use versus availability analysis did show a common preference for forbs by both *T. sirtalis* and *L. pipiens*, our analysis examining the influence of *L. pipiens* on *T. sirtalis* habitat selection demonstrated that the abundance of *T. sirtalis* in both grids and sectors of grids was unrelated to the abundance of *L. pipiens*. The exact sectors within grids where frogs were found did not coincide with the sectors where we found snakes. This suggests that, at a fine scale, *T. sirtalis* are not more likely to be found in locations where *L. pipiens* is found, despite this apparent shared habitat preference.

We found no effect of *L. pipiens* abundance on *T. sirtalis* habitat use, but this may be due to the low abundance of frogs in 2015 (Table 1). Indeed, habitat selection by *L. pipiens* is strongly related to moisture content in the soil (Blomquist and Hunter 2009). Whereas 2014 was a very wet year, 2015 was a very dry year, which likely influenced the abundance of *L. pipiens* that we encountered on our grids. Although it has been suggested that habitat use by snakes might be linked to amphibian presence (Robertson and Weatherhead 1992), other evidence suggests that daily habitat use by snakes is not linked to food abundance because snakes generally eat infrequently and are not limited by food (Halliday and Blouin-Demers 2017). Long-term data with a much larger sample size would be required to truly test this hypothesis given the low abundance of snakes and the large fluctuations in frog abundance from year to year. Frogs are also just one food source for *T. sirtalis*; their second most consumed food is earthworms, and their third through fifth most consumed food items are sal-

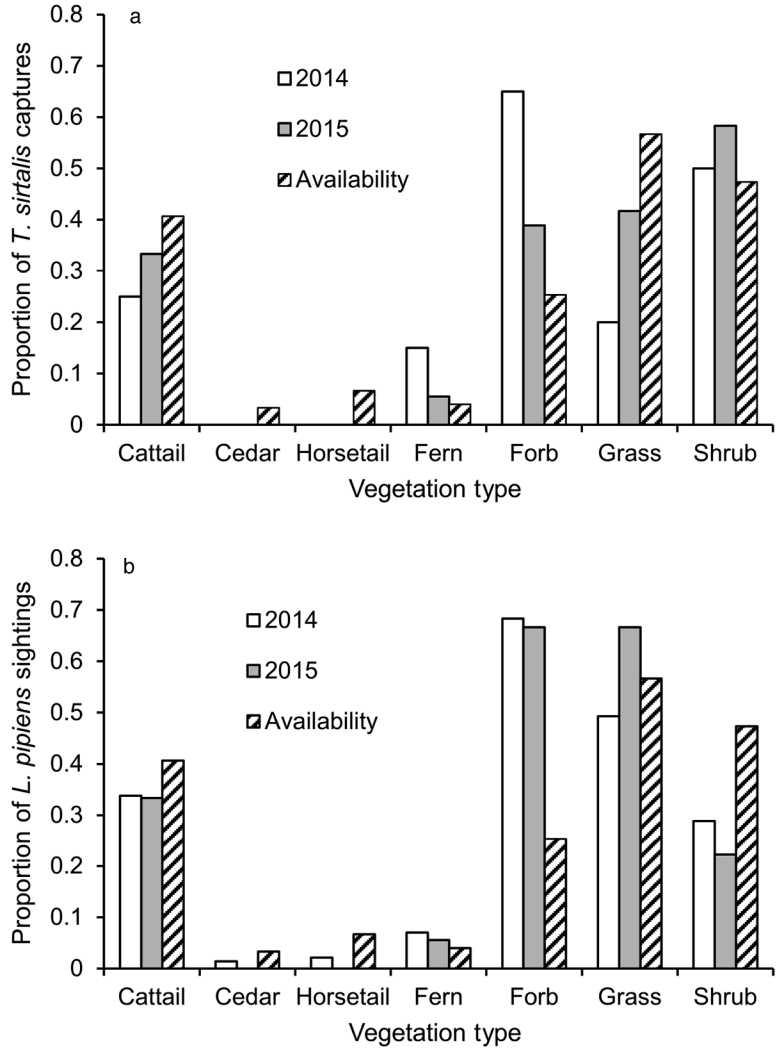

FIGURE 2. The proportion of captures of Common Gartersnakes (*Thamnophis sirtalis*; a) and sightings of Northern Leopard Frogs (*Lithobates pipiens*; b) in 1-ha study grids with different vegetation types in 2014 (white bars) and 2015 (grey bars) near Ottawa, Ontario, Canada. Hatched bars represent the proportion of sectors from all grids with each vegetation type (availability).

amanders, fishes, and small mammals (reviewed in Halliday 2016). Therefore, to truly test the hypothesis that food abundance is important in habitat selection, future studies should track the abundance of these other prey items in relation to the habitat selection of *T. sirtalis*. If *T. sirtalis* only spend a small amount of time hunting and eating prey, then the overall habitat selection that we observed would not reflect their choice for hunting. Radio-telemetry studies, along with detailed information on the activities being performed in different habitats, is crucial for understanding the reasons that *T. sirtalis* use different habitats.

The presence of water was not important to the habitat use of *T. sirtalis* in this study. This is despite water being important in previous habitat selection studies of *T. sirtalis* (Charland and Gregory 1995; Ernst and Ernst 2003), where they avoided deep water, but were still found in close proximity to water. Water levels in our study differed drastically in space and time. 2015 was a very dry year, and all of the water on a few grids completely disappeared by the end of August. In 2014, water levels remained high for the entire season. Given the few snake captures, this made it difficult to detect a water effect.

Detection probability of snakes and frogs likely differed between different vegetation classes. For instance, tall cattails limited our ability to detect snakes to within 2 m, whereas we could detect snakes farther away in

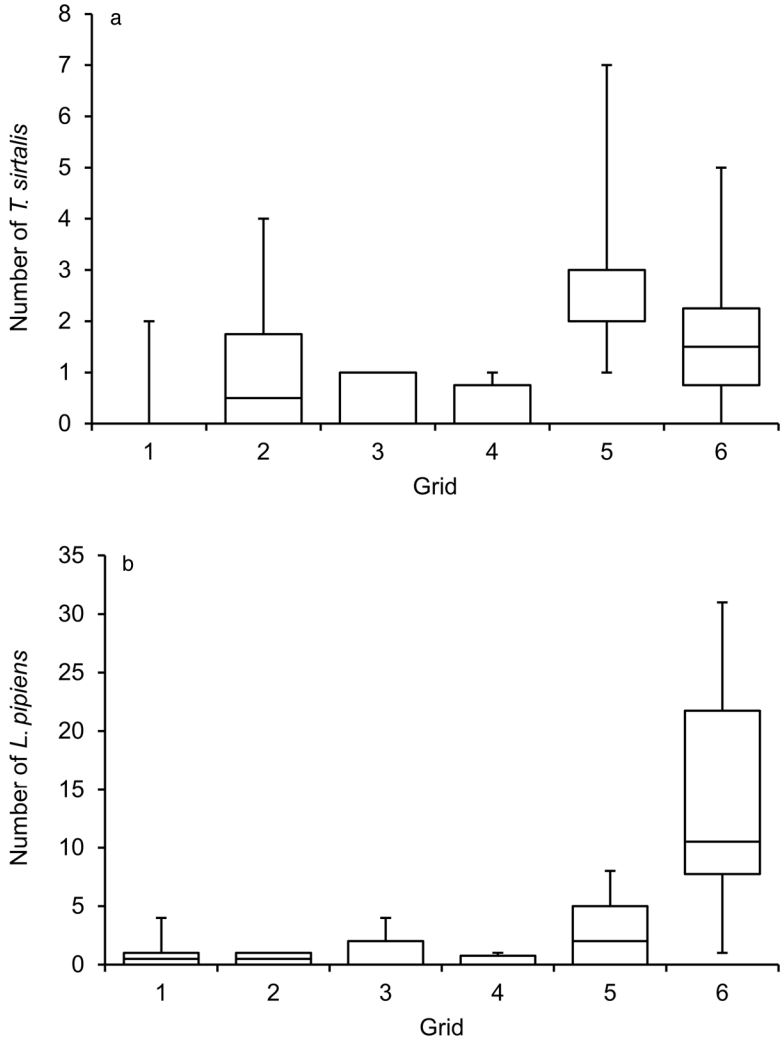

FIGURE 3. The number of Common Gartersnakes (*Thamnophis sirtalis*; a) and Northern Leopard Frogs (*Lithobates pipiens*; b) captured on each 1-ha study grid during each survey in 2014 and 2015 near Ottawa, Ontario, Canada. The line within the box is the median, the box represents the interquartile range, and the whiskers represent minimum and maximum values.

habitats with low vegetation. Snakes also effectively hid in tall grass, but tended to flee these areas when we approached, making it easier to detect them. It is therefore possible that this detection bias between habitats affected our results. However, regardless of habitat type, we kept a 2 m spacing between individuals for all surveys, and therefore did not rely on being able to detect snakes at long distances. Although this would not fully remove any potential bias, it should have helped to minimize detection bias between habitats. Future studies could use radio-telemetry to measure habitat selection by *T. sirtalis* in these habitats, and could also estimate observation bias by estimating the ability to visually find a radio-tagged snake in these habitats. Radio-telemetry also comes with its own biases, however, related to generally small sample sizes, limits on the size of snakes that can be studied, and issues related to implanting or affixing transmitters to snakes. We therefore recommend using data from a combination of methods, including visual surveys like ours and radio-telemetry.

In conclusion, vegetation structure is important to the habitat selection of *T. sirtalis*, likely because of its effect on microhabitat quality for activities like basking and hiding. *Lithobates pipiens* abundance and water cover were not important to the habitat selection of *T. sirtalis* in our study, but long-term data would be required to truly test the importance of these factors in

habitat selection due to their high variance within and between years.

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SUPPLEMENTARY MATERIAL:

TABLE S1. Model selection and final model output for general linear mixed effects models examining the presence/absence of Common Gartersnakes (*Thamnophis sirtalis*; Ts) based on habitat features and the presence/absence or abundance of Northern Leopard Frogs (*Lithobates pipiens*; Lp).

TABLE S2. Model selection and final model output for general linear mixed effects models examining the abundance of Common Gartersnakes (*Thamnophis sirtalis*; Ts) in study grids over two years near Ottawa, Ontario, Canada.

TABLE S3. Habitat use versus habitat availability for Common Gartersnakes (*Thamnophis sirtalis*, top) and Northern Leopard Frogs (*Lithobates pipiens*, bottom) selecting habitats near Ottawa, Ontario, Canada.

TABLE S4. Model selection and final model output for general linear mixed effects models examining the presence/absence of Northern Leopard Frogs (*Lithobates pipiens*; Lp) based on different habitat features.

TABLE S5. Model selection and final model output for general linear mixed effects models examining the abundance of Northern Leopard Frogs (*Lithobates pipiens*; Lp) in different study grids over two years near Ottawa, Ontario, Canada.