Northern snakes are more abundant in old fields than in forest

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i. **Abstract**

Temperature is one of the most important factors regulating habitat selection by ectotherms. By using behavioural thermoregulation, reptiles maintain their preferred body temperature and optimize their fitness. At northern latitudes, small colubrids rarely use forest habitat because of thermal constraints. In thermally challenging environments, open habitats such as old fields offer higher thermal quality than forests. I studied two northern colubrid snakes, *Storeria occipitomaculata* and *Thamnophis sirtalis,* to test the hypothesis that small northern snakes should be more abundant in open than in closed habitats because open habitats provide better opportunities for thermoregulation. Snakes were sampled with tin and plywood coverboards. Snakes were indeed more abundant in old fields than in forests, and fields provided higher thermal quality. Most snakes were captured in spring and summer (May – August), when temperatures were highest. *Storeria occipitomaculata* significantly preferred tin over plywood coverboards. I confirmed the strong preference for open habitats in northern snakes.

ii. **Acknowledgements**

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This is dedicated to Gilberto Cardinal-Fernandes, thank you for supporting me and being the greatest friend one could ask for.

Northern snakes are more abundant in old fields than in forest

1. Introduction

A common conception in ecology is that a species' relative abundance is highest at the center of its distribution and gradually decreases towards the edge. This is known as the "abundant center hypothesis" (Brown, 1984; Sagarin et al. 2006). However, several studies addressing this hypothesis have provided limited support for this pattern of spatial abundance. Tuya et al. (2008) refuted the hypothesis as a general rule of thumb in 6 out of 8 fish species. Out of 145 separate studies testing the "abundant center hypothesis" hypothesis, only 56 (39%) supported it (Sagarin & Gaines, 2002). Eckert et al. (2008) evaluated a total of 134 studies testing for declines in within-population genetic diversity and increases in among-population differentiation towards range margins. Although 64.2% of studies detected the expected decline in diversity and 70.2% showed increased differentiation, the difference in genetic diversity was not large between peripheral and central populations. Moreover, these studies had strong taxonomic and biogeographical biases, implying that generalization of the hypothesis may not yet be warranted (Samis & Lougheed, 2008).

The spatial distribution of reptiles appears much more complex than predicted by the "abundant center hypothesis", being influenced by numerous factors, such as prey density (Madsen & Shine, 1996), availability of hibernation sites (Reinert & Kodrich, 1982) and proximity to retreat sites (Martino et al., 2011). In terrestrial squamates, however, temperature is considered to be one of the most important factor regulating the selection of habitats (Reinert, 1993). In ectothermic animals, the necessity to maintain an adequate body temperature is vital for physiological and developmental processes (Peterson et al., 1993). Indeed, temperature regulation directly affects physiological, reproductive, and ecological performance (Huey, 1982).

Body temperature has been shown to influence defensive responses in lizards, indirectly affecting their fitness (Hertz et al., 1982). Some of the behavioural strategies used by these animals are active thermoregulation by exposure to sunlight and modifying their posture (Bauwens et al., 1996; Huey 1982), which allow the animals to maintain a body temperature optimizing their fitness (Huey & Kingsolver, 1989). By adjusting microhabitat selection and time of activity, ectotherms can gain heat from the environment and optimize their thermoregulation (Krohmer, 1989; Huey et al., 1989). Thermoregulation strategies are strongly influenced by the thermal quality of the environment (Huey and Slatkin, 1976).

In northern latitudes, small colubrids seem to use forest habitat very rarely, probably because of thermal constraints (Charland & Gregory, 1995; Halliday & Blouin-Demers, 2015). In black ratsnakes (*Elaphe obsoleta*), forest edges provide the best opportunities for thermoregulation, offering both basking and a safe retreat when digesting prey (Blouin-Demers & Weatherhead, 2001). Milksnakes (*Lampropeltis triangulum*) prefer open habitats, such as old fields, with high thermal quality (Row & Blouin-Demers, 2006a). Since forests are dense and do not allow proper sunlight exposure, snakes should use open habitats because they offer a larger variety of temperature, allowing them to alternate between basking in the sun and using natural covers (Row & Blouin-Demers, 2006b).

Thamnophis sirtalis and *Storeria occipitomaculata*, both small northern snakes, have mean preferred body temperatures of 25.5–27.4°C and ≈ 26.5°C, respectively (Halliday & Blouin-Demers, 2016; Brattstrom, 1965). To thermoregulate properly, these snakes have to scout their environment and chose their habitat according to their preferred temperature (Peterson, 1987). I tested the hypothesis that small northern snakes should be more abundant in open than in closed habitats because open habitats provide better opportunities for thermoregulation. I predicted that the number of captures should be significantly higher in old fields than in forests.

Coverboards are effective for sampling snakes (Ryan et al., 2002; Grant et al., 1992; Houze & Chandler, 2002), particularly cryptic species (Halliday & Blouin-Demers, 2015). Coverboards of different sizes (Hecnar & Hecnar, 2011) and type of material (Engelsoft & Ovaska, 2000) can attract different snake species according to their microhabitat preferences; coverboards can differ for example in the moisture and temperature range they offer (Houze & Chandler, 2002; Hyde & Simons, 2001). Coverboards are often made using tin or plywood. Tin being a better thermal conductor than plywood, it was more effective to sample *Thamnophis sirtalis*, *Thamnophis elegans* and *Contia tenuis* in British-Columbia (Engelstoft & Ovaska, 2000). Coverboards are preferred over traps because they are economical and safe (Ryan et al., 2002). A secondary objective of my study was to quantify the efficacy of tin and plywood coverboards.

2. Materials and methods

This study took place in Gatineau Park (45.5833° N, 76.0000° W), where the snakes were sampled at 4 sites in summer 2015: Meech Creek Valley (45.3418° N, 75.5326° W), Pilon Road, (45.3336° N, 76.326° W), Denison Lake Dam (45.2755° N, 75.4714° W), and Luskville Falls (45.3208° N, 75.5926° W). Although *Storeria occipitomaculata*, *Thamnophis sirtalis*, *Liochlorophis vernalis*, *Diadophis punctatus*, and *Lampropeltis triangulum* were all captured, we only obtained sufficient sample sizes for analysis for two species: *Thamnophis sirtalis* and *Storeria occipitomaculata*. The plant community in the old fields consisted mainly of *Aster* sp., *Rhamnus* sp., *Asclepias* sp., *Cirsium* sp. and *Poa* sp. All forests were mostly composed of *Betula papyrifera*, *Acer saccharum*, and *Fagus grandifolia*.

At each of the 4 sites, I set up 200 meters long transects with pairs of coverboards (one tin, one plywood) installed every 10 meters (Fig. 1). At each site, the transects were parallel to and 50 m from the edge between old field and forest, one transect in the field and one transect in the forest. Thus, a total of 320 coverboards were deployed: 280 coverboards were 90 x 60 cm, and 40 coverboards were 45 x 45 cm.

I sampled snakes from 14 May 2015 to 16 November 2015, for a total of 26 weeks. All coverboards were checked weekly between 0800 h and 1800 h. The four sites were visited on the same day, with a weekly rotation in the order of the visits. The day of the week when the visits were scheduled varied from week to week to choose the best possible weather : sunny days with moderately high temperatures (around 26-28°C). Snakes were hand captured and data were acquired directly in the field. Each individual was marked by branding one ventral scale with a medical cautery unit (Bovie Aaron Low-Temp Reusable Cautery Unit, Clearwater, Florida; Winne et al., 2006). The date, time, sex, snout-vent length, temperature, temperature under the coverboard and habitat type were recorded for each snake captured. Individuals were then released at their point of capture. I placed 18 temperature data loggers (Dallas iButton thermochron (Sunnyvale, California, USA), model DS1921L; 3 g) under coverboards of both materials and in both habitats across the four sites. The loggers were programmed to measure the temperature on the hour for two periods: from 2400 h on 12 May 2015 to 1500 h on 30 July 2015 and from 0600 h on 10 September 2015 to 0600 h on 23 October 2015.

For both species, I compared the number of snakes captured in forest to the number of snakes captured in field using generalized linear mixed-effects models with a Poisson distribution in R (package: lme4; function: glmer; family: poisson; Bates et al. 2012). I used a Poisson distribution because the data were zero inflated. Month, habitat, time of capture, temperature, coverboard material, and all interactions were fixed effects, and site identity was a random effect.

For both species, I examined the snout-vent length of snakes captured in forest and in field under tin and plywood coverboards using linear mixed-effects models in R (R Core Team, 2012; package: nlme; function: lme; Pinheiro et al., 2012). Month, habitat, coverboard material, time of capture, temperature and all interactions were fixed effects, and site identity was a random effect.

I compared maximum temperature under tin and plywood coverboards in forest and old field using linear mixed-effects models in R (R Core Team, 2012; package: nlme; function: lme; Pinheiro et al., 2012). Habitat, cover type, and all interactions were fixed effects and site identity was a random effect. Multiple comparisons were considered significant when $p < 0.05$.

3. Results

A total of 355 snakes of 5 species were captured during the 26 weekly visits. On average, I captured 14 snakes per visit. Captures rate remained constant from May until late August and slowly started decreasing until November. *Thamnophis sirtalis* (n = 90) and *Storeria occipitomaculata* (n = 242) were the two most abundant snake species (Fig. 3). Less often captured snake species included *Liochlorophis vernalis* (n = 2), *Diadophis punctatus* (n = 2), and *Lampropeltis triangulum* (n = 17).

Controlling for the effects of month, habitat, and time of capture, I captured significantly more *T. sirtalis* and *S. occipitomaculata* in field than in forest (*T. sirtalis*: $z = 4.47$, $p < 0.001$; *S. occipitomaculata*: $z = 9.196$, $p < 0.001$, Fig. 4). In fact, only 1 *T. sirtalis* and 7 *S. occipitomaculata* were captured in forest (Fig. 2). I also captured more snakes in mid-season than in early and late season (*T. sirtalis*: $z = 2.42$, $p < 0.0157$, Fig. 5; *S. occipitomaculata*: $z = 2.875$, $p < 0.004$, Fig. 6). While *T. sirtalis* did not seem to have a preference for tin or plywood coverboards ($z = 0.11$, $p < 0.91$, Fig. 4), I captured more *S. occipitomaculata* under tin coverboards than under plywood coverboards ($z = 5.78$, $p < 0.001$, Fig. 4). Although the time of the day had a weak effect, significantly more *T. sirtalis* were captured later in the day ($z = 2.44$, $p < 0.02$).

The length of snakes captured did not vary significantly between tin and plywood coverboards (*T. sirtalis*: $t = 0.69$, $p = 0.49$; *S. occipitomaculata*: $t = 0.22$, $p = 0.82$) or between forest and field (*T. sirtalis*: $t = 0.11$, $p = 0.91$; *S. occipitomaculata*: $t = 0.55$, $p = 0.58$, Fig. 7). The longest individuals of both species were captured early in the season, especially in May, June, and July (*T. sirtalis*: $t = 3.54$, $p < 0.001$, Fig. 8; *S. occipitomaculata*: $t = 3.81$, $p < 0.001$, Fig. 9). Both the time of capture and the temperature had no significant effect on the length of *T. sirtalis* captured ($t = 0.92$, $p = 0.36$; $t = 1.35$, $p = 0.18$, respectively). However, while the time of capture had no significant effect on the length of *S. occipitomaculata* captured ($t = 0.84$, $p = 0.40$), longer individuals were captured as temperature rose; with every 2°C increase, individuals were 2.59 mm longer ($t = 2.75$, $p = 0.007$).

Temperature did not vary significantly between plywood and tin coverboards ($t = 0.16$, $p = 0.87$). Temperature varied significantly between coverboards in forest and those in field only in the warmer months (May, June and July). During these months, temperature under coverboards in field were 8.8°C higher than those under coverboards in forest (t = 3.46, p = 0.001, Fig. 10). Coverboards in forests never warmed to the preferred temperature range of either *S. occipitomaculata* or *T. sirtalis* (Fig. 10).

4. Discussion

Both *Thamnophis sirtalis* and *Storeria occipitomaculata* preferred old fields habitat over forests habitat, as observed in previous studies of other snakes (*Lampropeltis triangulum*, *Pituophis catenifer*, *Thamnophis* spp., *Heterodon platirhinos* and *Contia tenuis*) (Row & Blouin-Demers, 2006b; Charland & Gregory, 1995; Kapfer et al, 2008; Lagory et al., 2009), and old fields offered higher thermal quality. *S. occipitomaculata* very rarely used forest habitat and *T. sirtalis* was not spotted once in forest transects. Old fields offered significantly higher temperatures than forests, particularly in May, June, and July. This supports my hypothesis that northern snakes are more abundant in open habitats because of their high thermal quality, which allows efficient behavioural thermoregulation. Halliday & Blouin-Demers (2016) demonstrated that *Thamnophis sirtalis* prefers open habitats and that open habitats offer the highest thermal quality and increase fitness. Similarly, ratsnakes (*Elaphe obsoleta*) use open habitats to enhance fitness by improving locomotor performance and allowing avoidance of lethal temperatures (Blouin-Demers & Weatherhead, 2008). It is also important to note that while open habitats were the preferred habitat for northern snakes from May until October, forests can still be an important habitat. For example, Eastern Massasauga rattlesnakes (*Sistrurus c. catenatus*) preferred forests for hibernation and increased their use of open habitats in mid-summer (Harvey & Weatherhead, 2006).

Most and the largest *T. sirtalis* and *S. occipitomaculata* were captured in May, June, July, and August with a peak in June-July, which corresponds to the highest maximum temperatures. Since thermoregulation directly affects physiological, reproductive and ecological performance (Huey, 1982), it is likely that the high number of captures during warmer months are a result of high thermal quality. From May-August, high solar radiation heated up the coverboards in old fields, rendering them useful for behavioural thermoregulation.

The decrease in the size of snakes and in the frequency of captures in August most likely results from the emergence of juveniles and the migration of snakes to their hibernacula. Some *T. sirtalis* undergo an annual migration between summer and winter habitats and may return to their winter dens as early as late July until September (Larsen, 1987; Joy & Crews, 1987; Gregory & Stewart, 1975). Reproductive females stay in the summer habitat until they give birth (Larsen, 1987; Gregory, 1984). Therefore, the number of captures significantly decreasing in August in *S. occipitomaculata* and in September in *T. sirtalis* could indicate parturition followed by migration to the hibernacula. In fact, parturition occurred until August in *S. occipitomaculata* and until September in *T. sirtalis* (Meshaka, 2010). *S. occipitomaculata* populations in western Pennsylvania and northeastern Ohio have been observed to have an activity peak in June and July, followed by a peak in juveniles in September (Meshaka, 2010; Meshaka et al., 2008). *S. occipitomaculata* activity remained constant during May-August, diminished in September and surface activity ended by mid-October (Hulse et al. 2001). Thus, the seasonal activity patterns of *T. sirtalis* and *S. occipitomaculata* observed in this study match observations in precedent studies.

It is important to note that this study took place in a challenging thermal environment, where thermal quality is a really strong predictor of habitat selection. In more southern and tropical locations, snakes often use forest habitats (Luiselli & Capizzi, 1997; Steen et al., 2012; Baxley et al., 2011), indicating thermal quality is not the strongest predictor of habitat selection in warmer areas. Ratsnakes (*Elaphe obsoleta*) populations in Illinois, a less thermally challenging environment, used upland forest more and forest edges less than ratsnakes in Ontario (Carfagno & Weatherhead, 2006). Therefore, while northern populations of species such as *T. sirtalis* and *S. occipitomaculata* prefer open habitats for their thermal quality, southern populations of the same species or southern species might prefer different habitats for other reasons, such as prey density (Madsen & Shine, 1996; Wasko & Sasa, 2012) and proximity to retreat sites (Martino et al., 2011).

Tin was preferred over plywood coverboards by *Storeria occipitomaculata*, as observed in other snakes species (Engelstoft & Ovaska, 2000; Halliday & Blouin-Demers, 2015). Although Engelstoft & Ovaska (2000) explained this difference by tin being a better thermal conductor, I did not detect a significant difference between temperatures under tin and plywood coverboards. Furthermore, *Thamnophis sirtalis* did not show the preference for tin coverboards, but this might be due to limited captures (only 90 *T. sirtalis* were captured for 242 *S. occipitomaculata*). A possible explanation for the lack of difference in temperature between plywood and tin coverboards in this study may that I used mean maximal temperatures over monthly observations, which will not take account the more intricate hourly and daily variation between both materials.

In conclusion, open habitats such as old fields are where *Thamnophis sirtalis* and *Storeria occipitomaculata* were found in higher abundance in the course of this study. This confirms the preference of open fields, likely because they facilitate behavioural thermoregulation, in northern snakes. An important caveat must be made. Snakes were sampled with coverboards, and coverboards may be more attractive to snakes in open habitats than in closed habitats. For instance, I showed that coverboards in fields became warmer than coverboards in forest because they received more solar radiation. In fact, coverboards in forest never reached the preferred body temperature range of small northern snakes. Thus, it is possible that coverboards in field are used more than coverboards in forest because of their superior thermal quality. If that were to be the case, the number of captures under coverboards between habitats may not be an accurate reflection of the density of snakes between habitats. This potential bias clearly deserves further study.

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Appendix

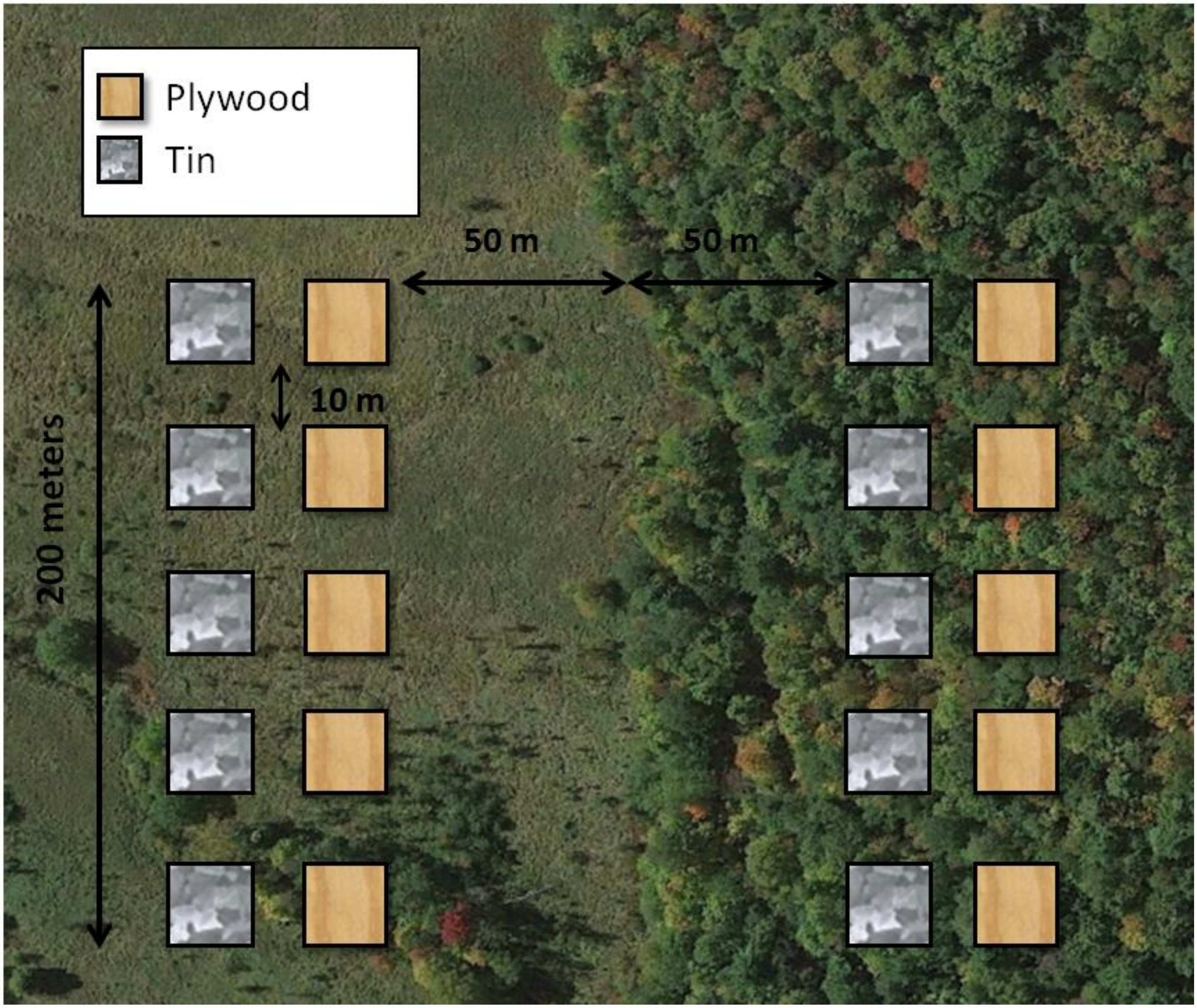

Figure 1. Diagram depicting the setup of coverboards transects in individual study plots.

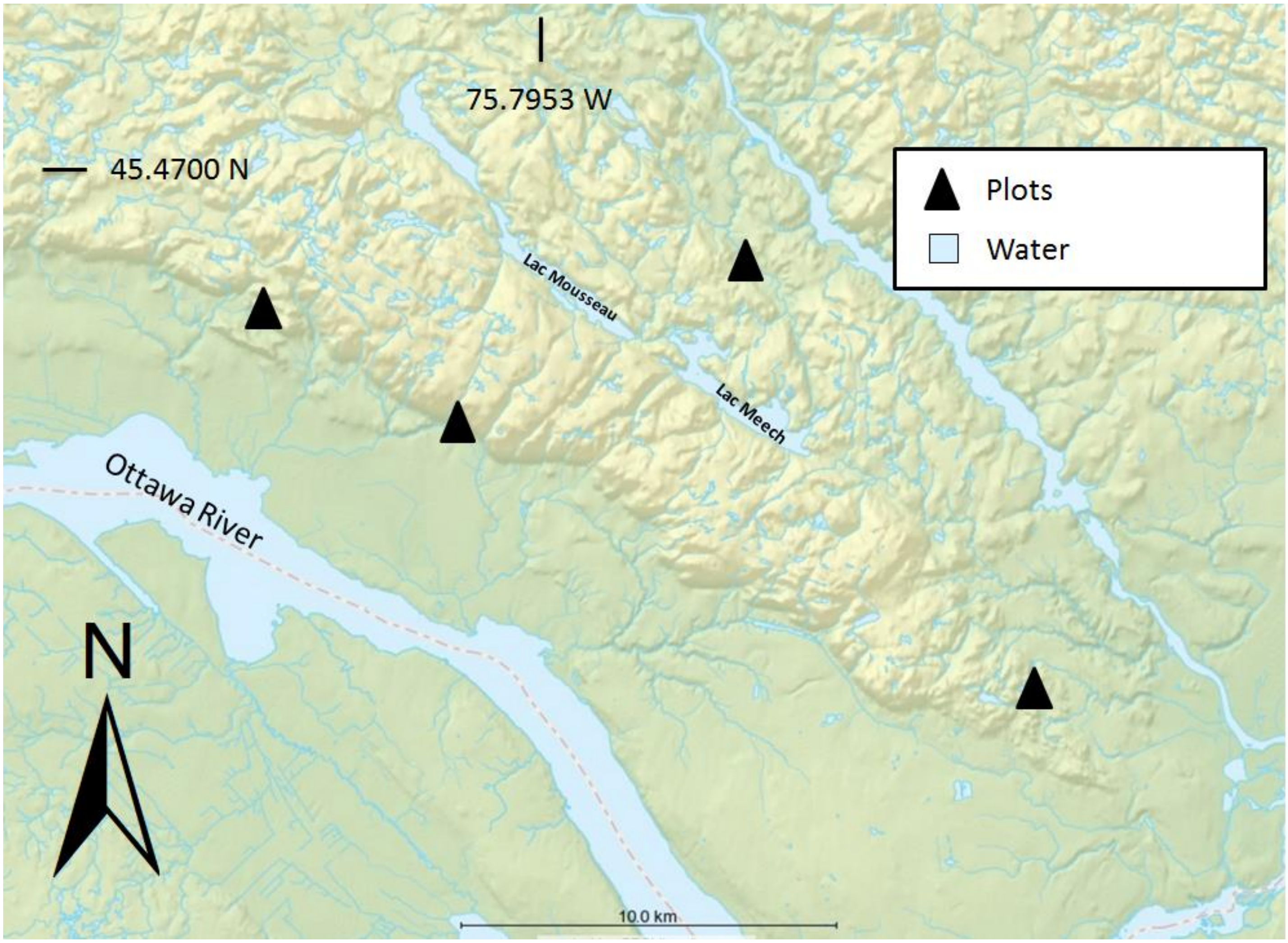

Figure 2. Layout of study plots depicting all four different sites in Gatineau Park, Quebec, Canada. Coordinates are in WGS 84.

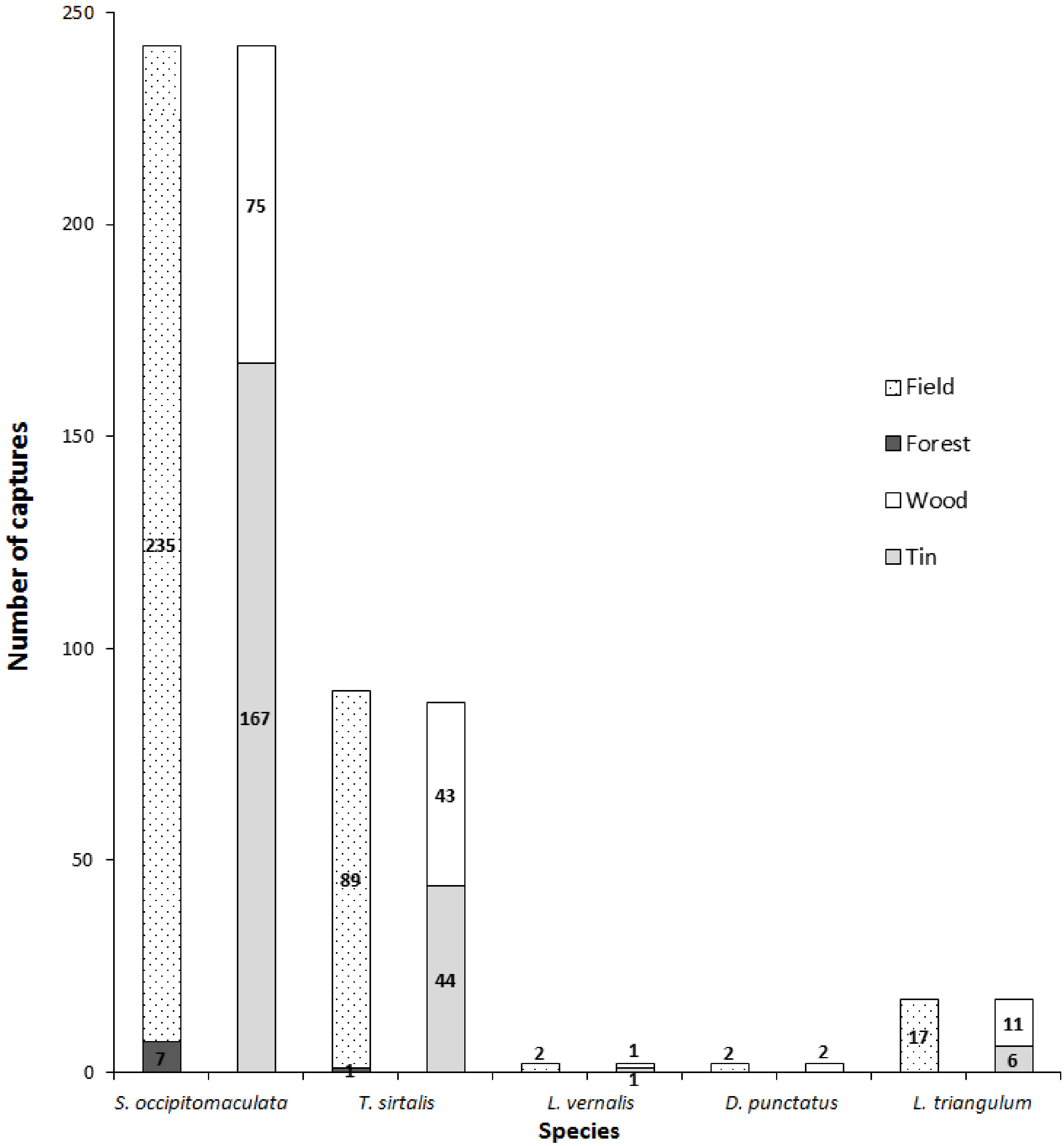

Figure 3. Summary of total number of captures in field and forest plots and under tin and plywood coverboards in Gatineau Park, Quebec, Canada. The sampling period lasted from May 14th 2015 to November 16th 2015, for a total of 26 sampling days.

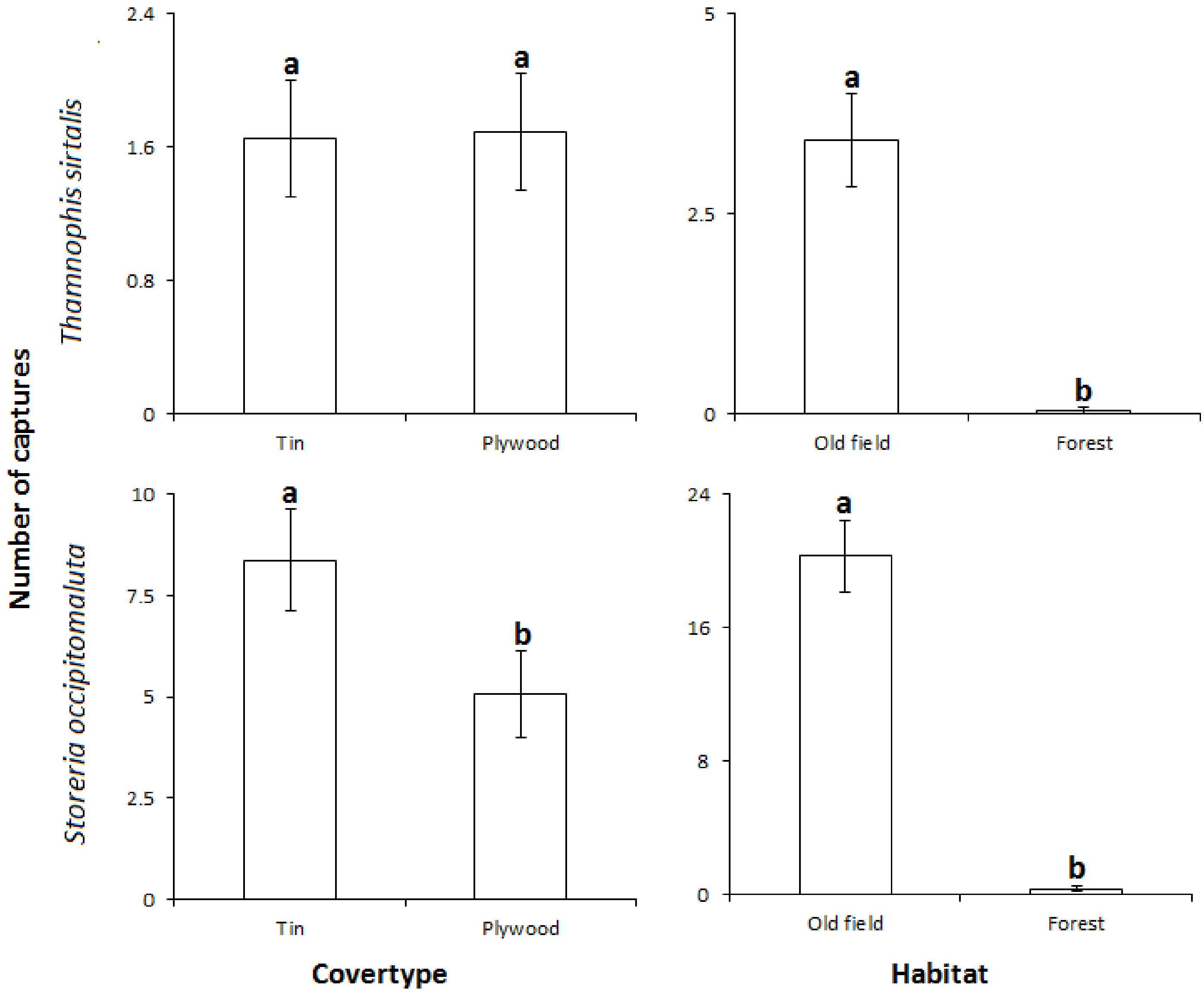

Figure 4. Number of captures for *Storeria occipitomaculata* (n= 242) and *Thamnophis sirtalis* (n= 90) under different coverboards type and in different habitats in Gatineau Park, Quebec, Canada. Each bar represents the mean value of daily captures across all four study plots for the entire sampling period. Means with the same letters are not significantly different at $p > 0.05$. The sampling period lasted from May 14th 2015 to November 16th 2015, for a total of 26 sampling days. Error bars represents the standard error.

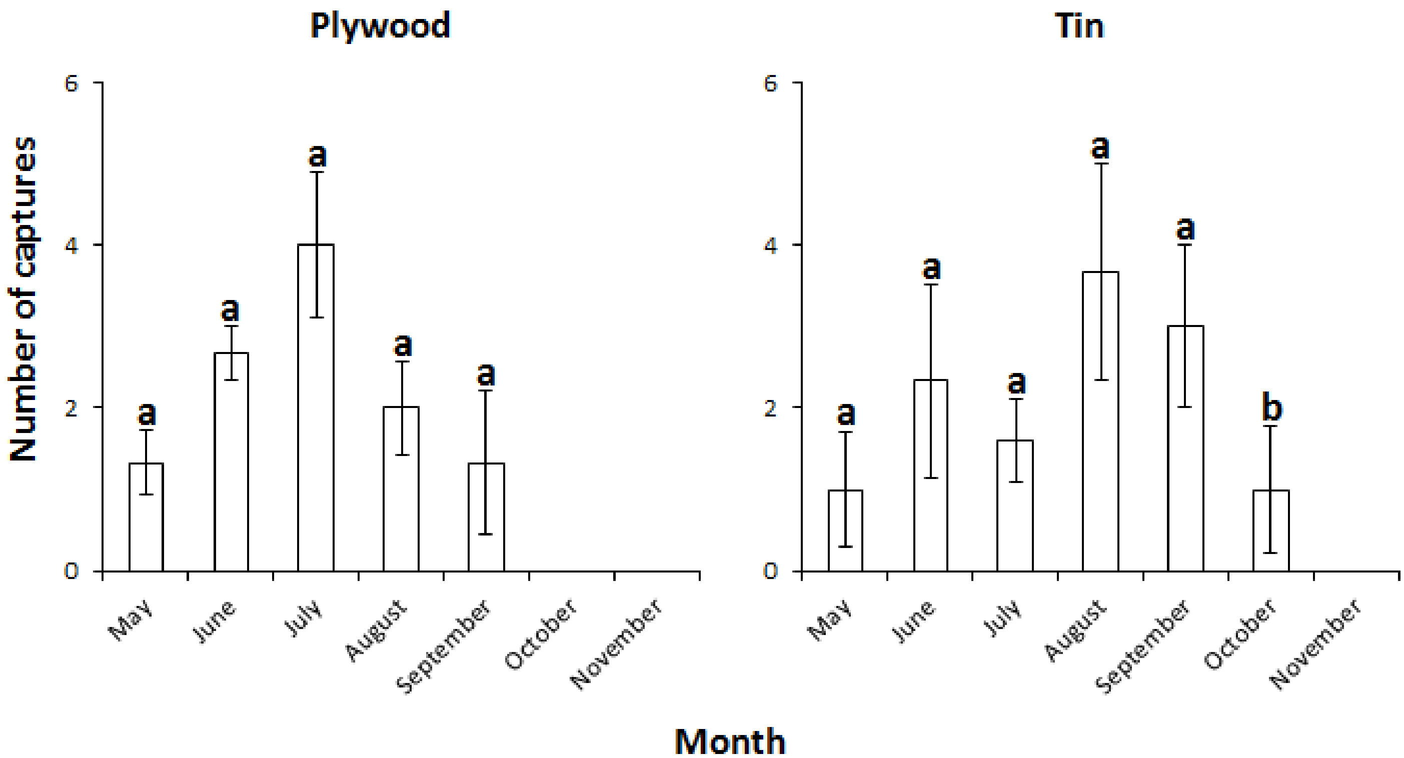

Figure 5. Number of captures by month for *Thamnophis sirtalis* (n=90) under different coverboards type in old field in Gatineau Park, Quebec, Canada. Each bar represents the mean value of monthly captures across all four study plots for the entire sampling period. Means with the same letters are not significantly different at $p > 0.05$. The sampling period lasted from May 14th 2015 to November 16th 2015, for a total of 26 sampling days. Error bars represents the standard error. Note that no snakes were detected in forest and in November.

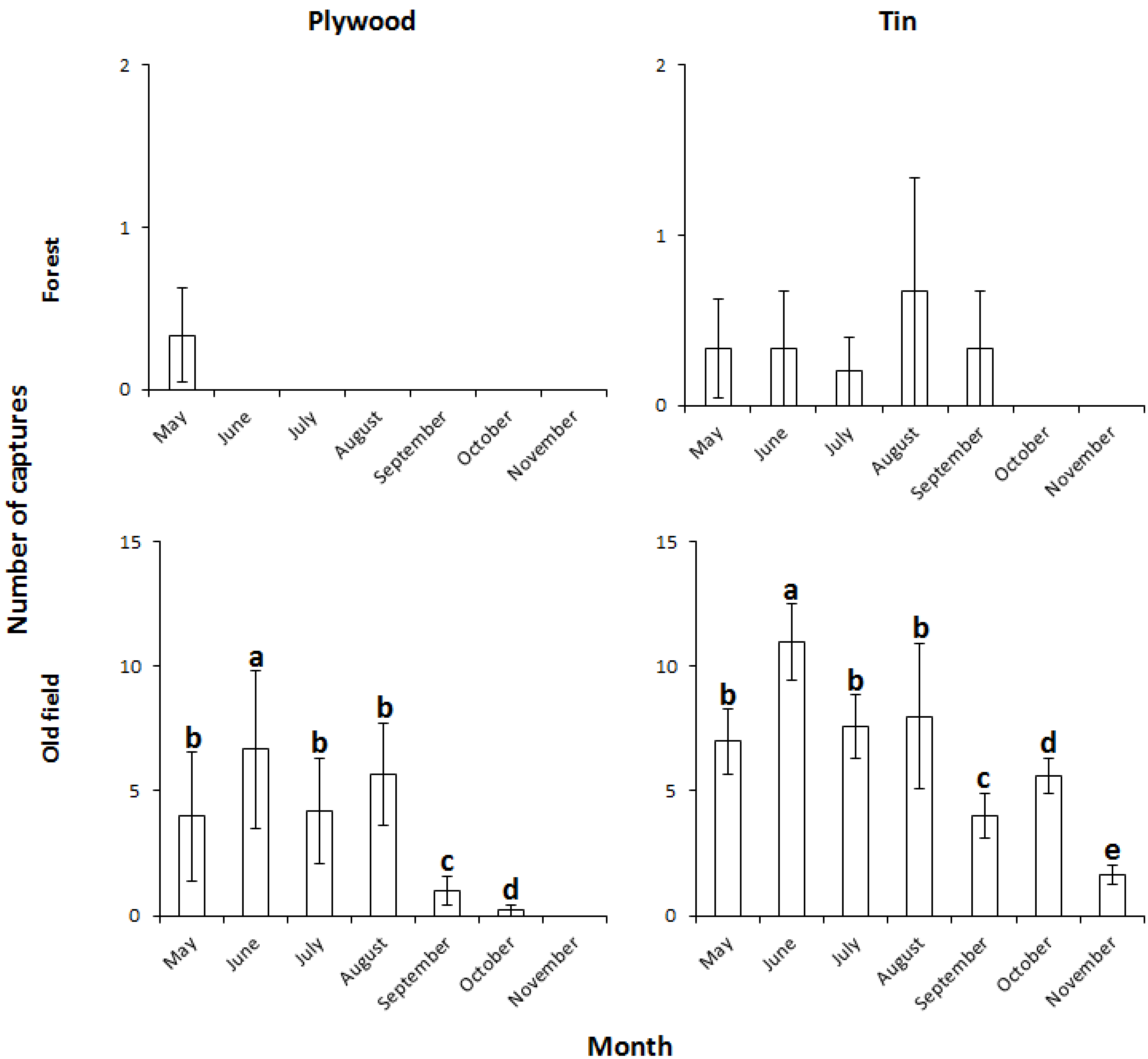

Figure 6. Number of captures by month for *Storeria occipitomaculata* (n=242) in under different coverboards type and in different habitats in Gatineau Park, Quebec, Canada. Means with the same letters are not significantly different at $p > 0.05$. Each bar represents the mean value of monthly captures across all four study plots for the entire sampling period. The sampling period lasted from May 14th 2015 to November 16th 2015, for a total of 26 sampling days. Error bars represents the standard error.

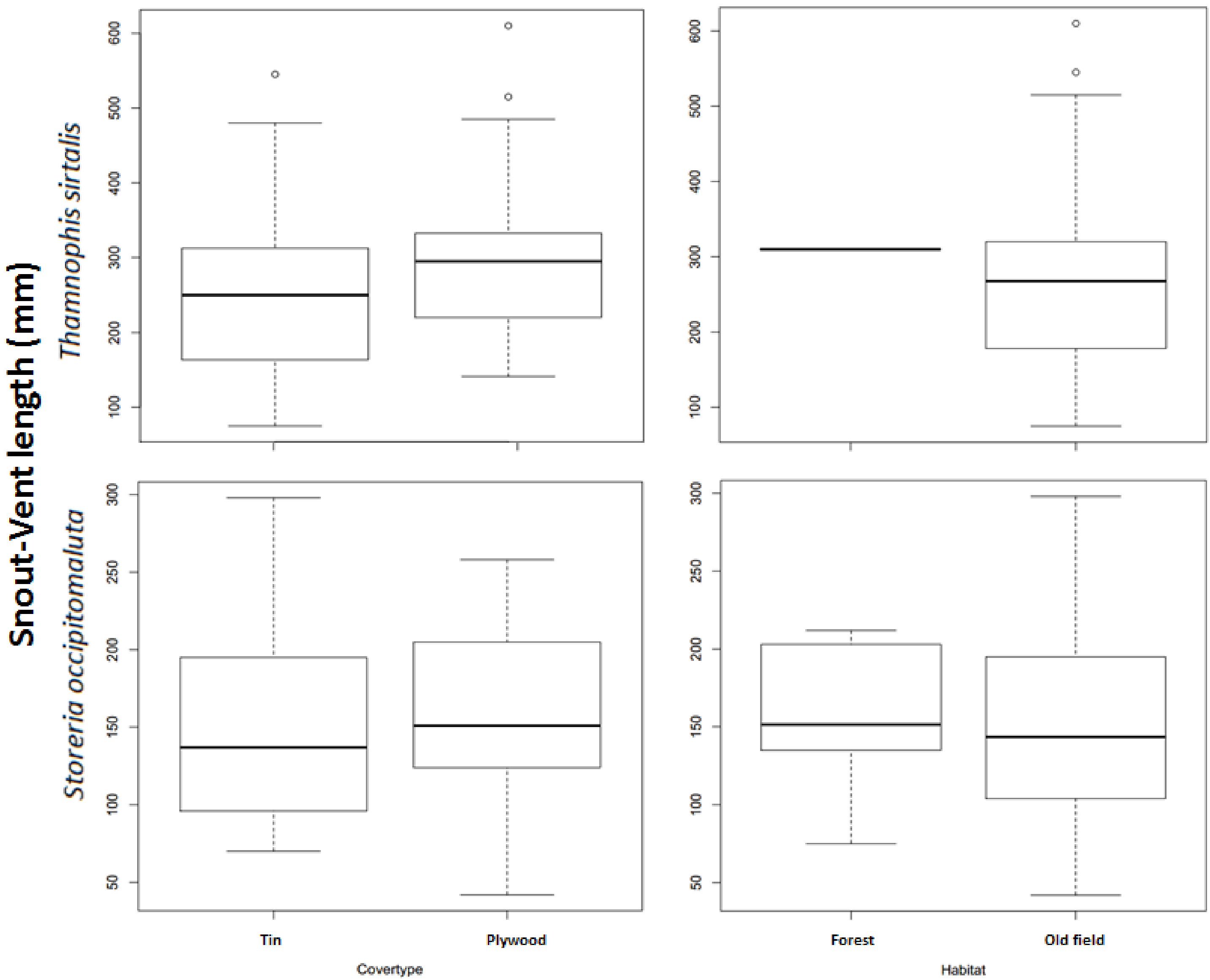

Figure 7. Snout-Vent length of *Thamnophis sirtalis* (n= 68) and *Storeria occipitomaculata* (n= 204) in forest and old field habitats in Gatineau Park, Quebec, Canada on study transects with tin and plywood coverboards. The sampling period lasted from May 14th 2015 to November 16th 2015, for a total of 26 sampling days.

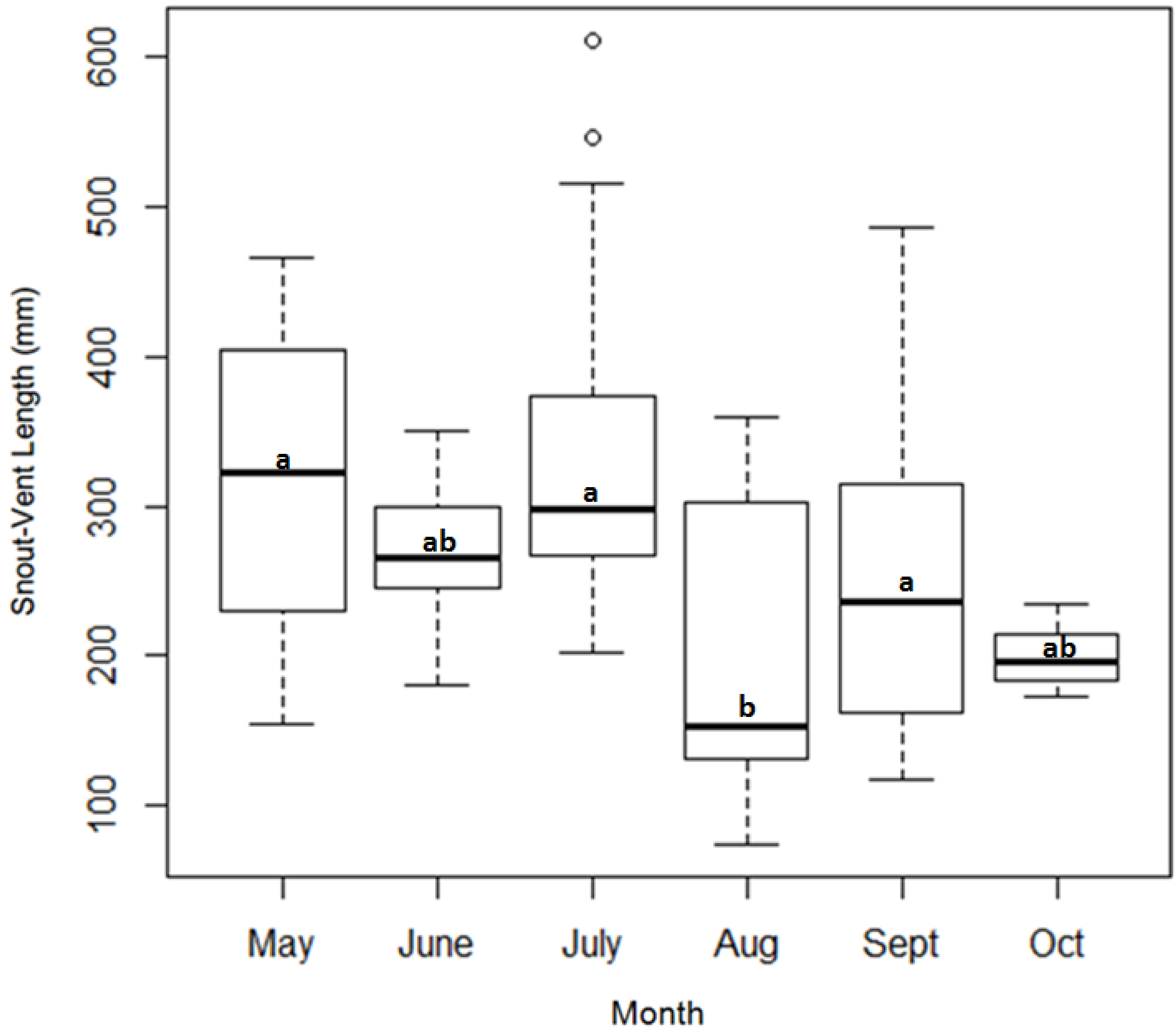

Figure 8. Monthly variation in snout-Vent length of *Thamnophis sirtalis* (n= 68) in forest and old field habitats in Gatineau Park, Quebec, Canada on study transects with tin and plywood coverboards. Means with the same letters are not significantly different at $p = 0.05$. The sampling period lasted from May 14th 2015 to November 16th 2015, for a total of 26 sampling days.

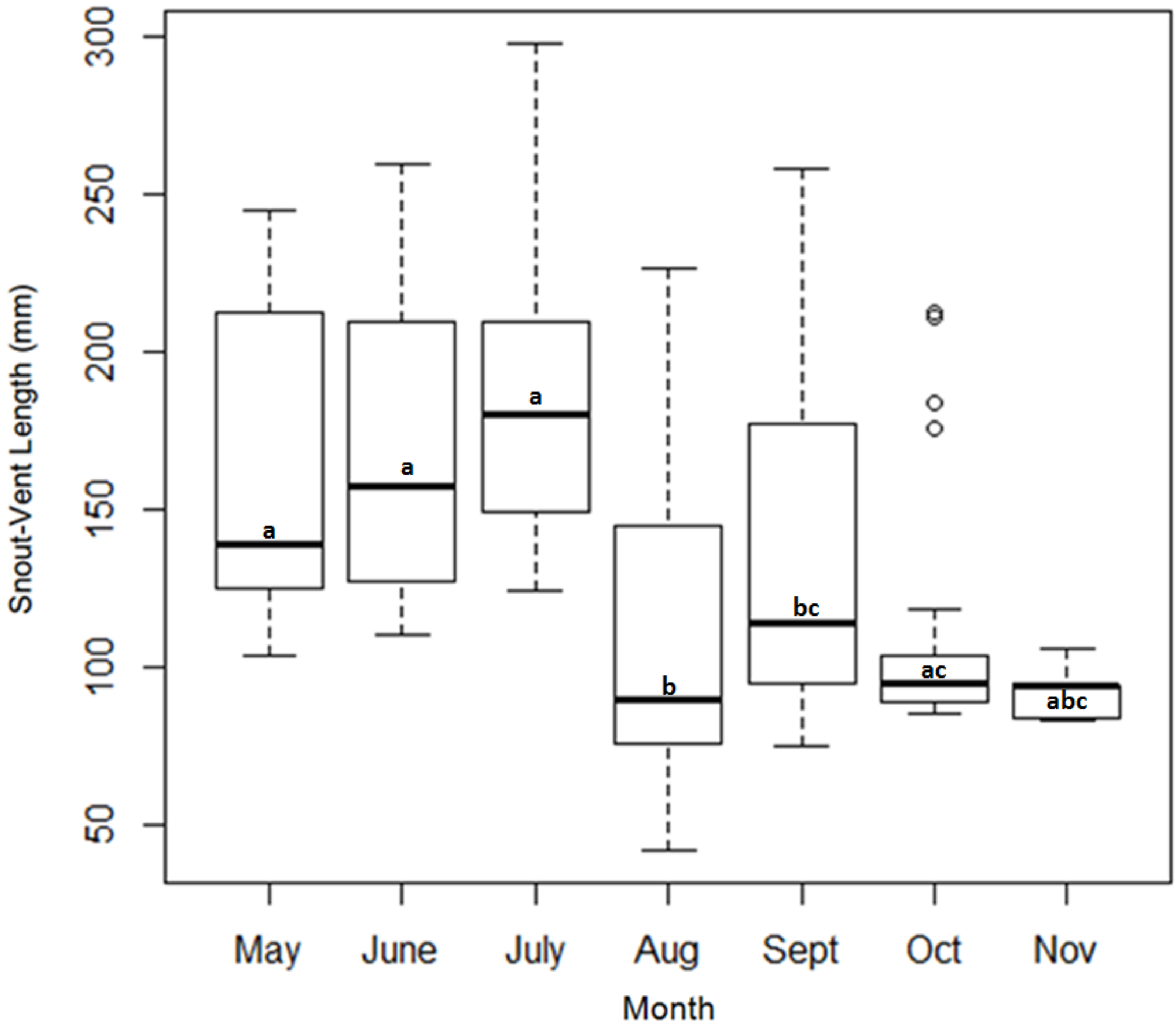

Figure 9. Monthly variation in snout-Vent length of *Storeria occipitomaculata (n= 204)* in forest and old field habitats in Gatineau Park, Quebec, Canada on study transects with tin and plywood coverboards. Means with the same letters are not significantly different at p = 0.05. The sampling period lasted from May 14th 2015 to November 16th 2015, for a total of 26 sampling days.

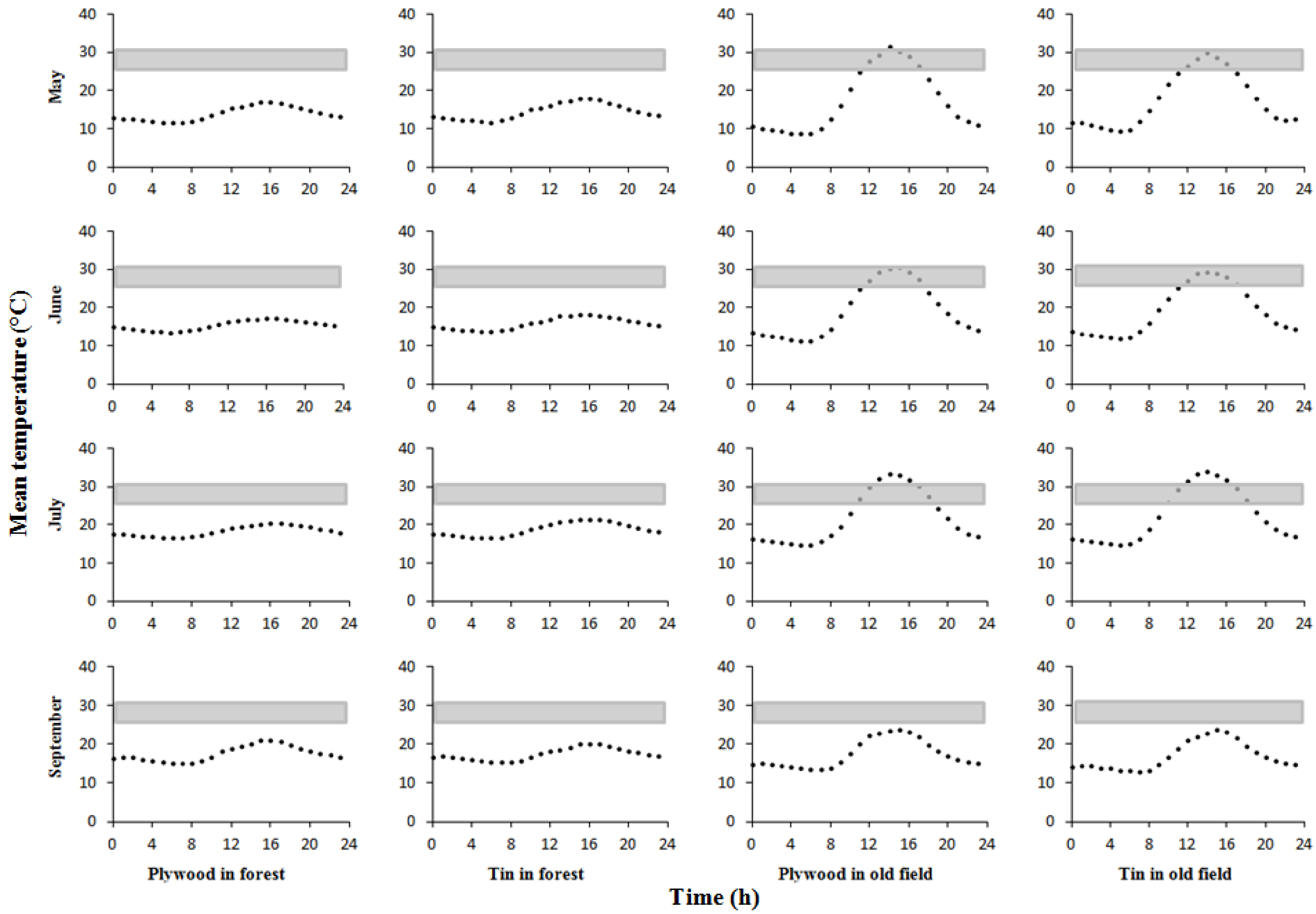

Figure 10. Average 24-h temperature profiles of each Ibutton data logger for each of the habitat and coverboard material type combinations for five months in Gatineau Park, Quebec, Canada. The grey rectangle represents the mean preferred temperature for *Thamnophis sirtalis* (24.5° -30.7 °C). N=20 days for May, 30 days for June and July and 19 days for September.

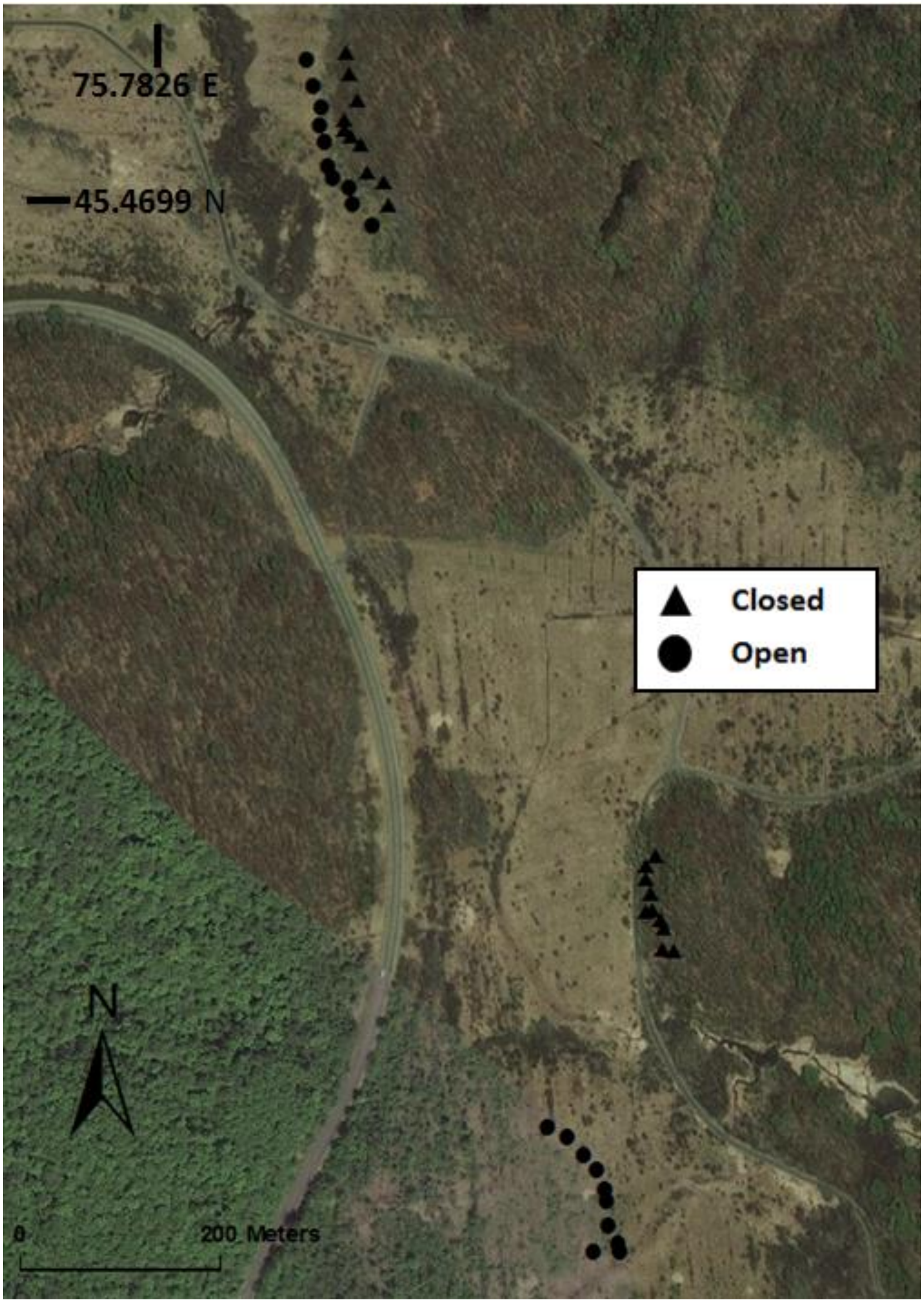

Figure 11. Layout of coverboard transects near the Denison Lake Dam in Gatineau Park, Quebec. Coordinates are in WGS 84.

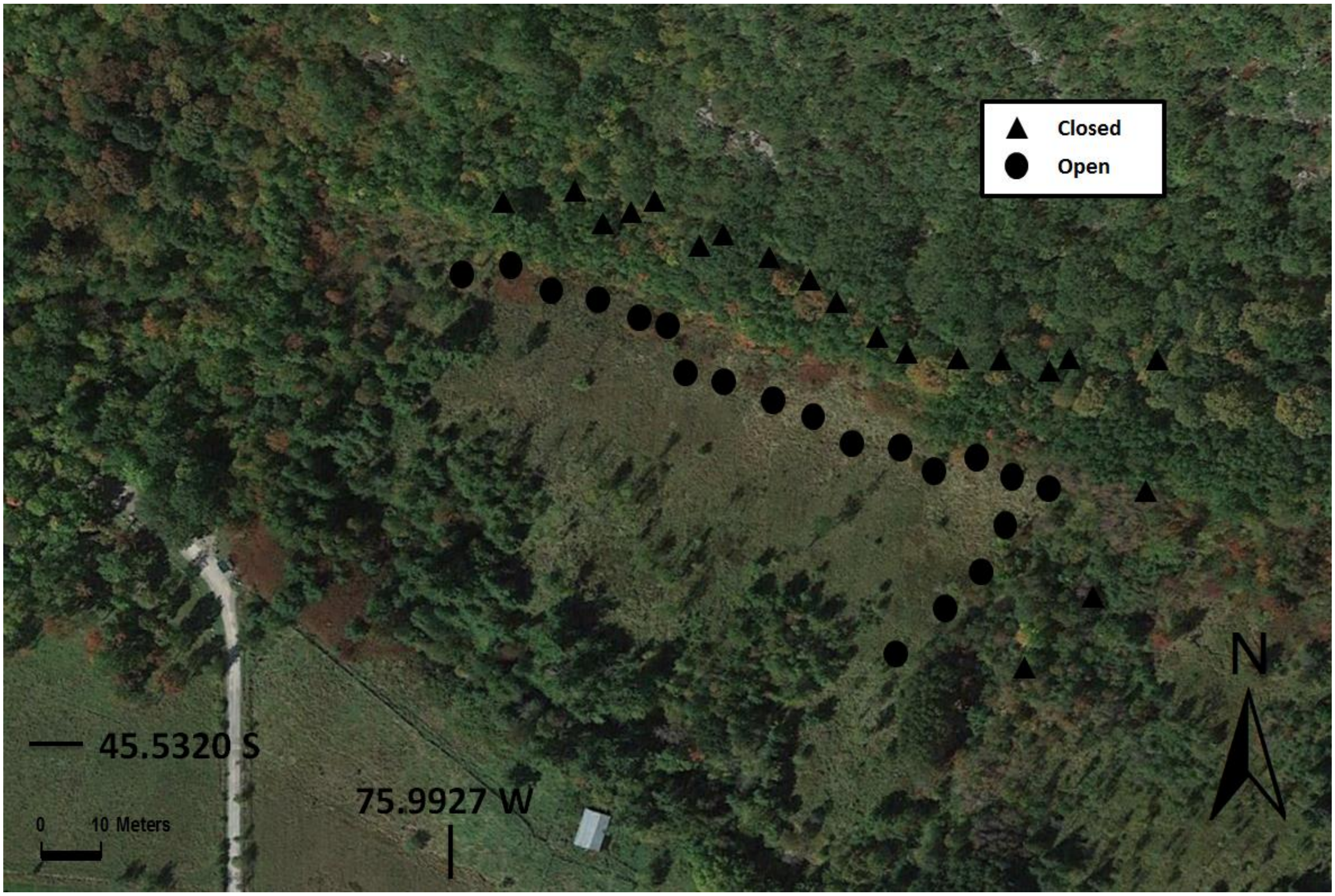

Figure 12. Layout of coverboard transects near at the Luskville Falls in Gatineau Park, Quebec. Coordinates are in WGS 84.

Figure 14. Layout of coverboard transects at the Meech Creek Valley in Gatineau Park, Quebec. Coordinates are in WGS 84.

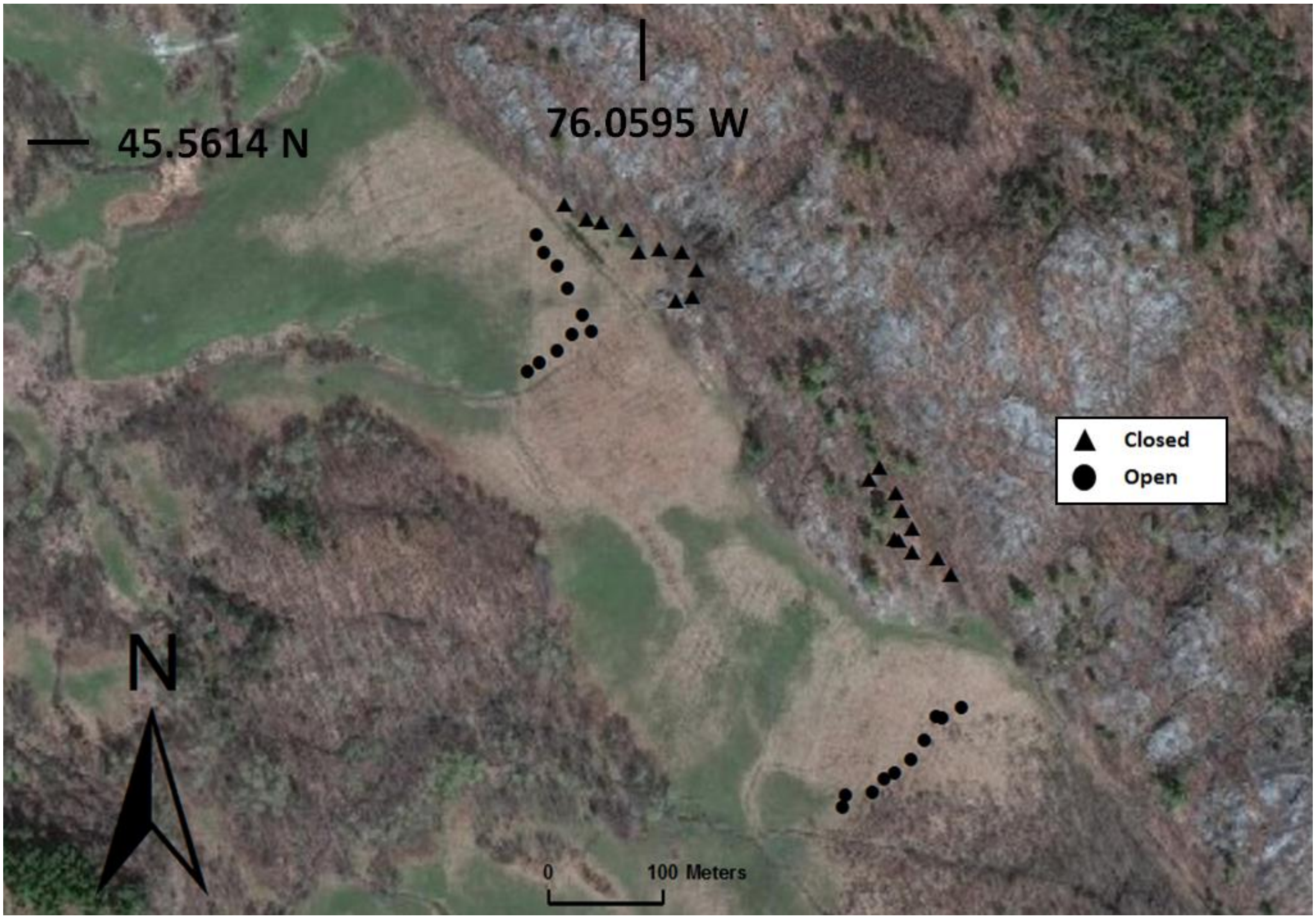

Figure 15. Layout of coverboard transects at Pilon road in Gatineau Park, Quebec. Coordinates are in WGS 84.