

## Snake Community Composition in Unmanaged Grasslands of Different Successional Ages at the James H. Barrow Biological Field Station

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**Abstract:** The historical destruction and fragmentation of grassland habitat has led to negative consequences for vertebrate taxa that rely on these ecologically rich ecosystems. Although the decline of some taxa such as grassland birds has been well documented, little is known about how grassland decline impacts snake communities. This study was conducted to assess differences in snake abundance and species richness in unmanaged grasslands of three successional ages at the James H. Barrow Biological Field Station (Portage County, OH): young (4–7 years), mid-successional (12–15 years), and old (>50 years). Ten corrugated metal and ten plywood cover boards were used at each site to address community and species-specific preferences for board type. Surveys were conducted weekly from June through August over four summers (2016–2019) in an effort to detect seasonal peaks in abundance and the effects of board maturity. Additionally, snake assemblages were compared during morning and evening surveys during a single summer to address differences in time of day. A total of 419 eastern garter snakes, 85 northern brown snakes, 172 eastern milk snakes, and 3 northern red-bellied snakes were captured across all years. Overall, both abundance and species richness were significantly higher in the youngest successional grassland, with the mid-successional and oldest successional site yielding similarly low diversity. Although both eastern garter snakes and eastern milk snakes were found in highest abundance in the youngest site, northern brown snakes were equally abundant in grasslands of each successional age. In the youngest successional site only, both abundance and species richness significantly increased across years, peaking at year three and remaining similar during year four, indicating that a threshold of diversity may be reached between 7 and 12 years of successional age. Because this trend was only observed in the youngest site and seasonal peaks were not observed for any species, it is unlikely that board maturity plays a role in detection of snakes. No significant differences in snake abundance or species richness were observed for cover board type or time of day of survey. Overall, our results suggest that both metal and plywood cover boards can be effective to survey snake assemblages, and evening sampling could yield similar results to morning sampling. However, these results are limited to one geographical location. Further, the maintenance of young successional habitat may be necessary to promote grassland snake diversity, but species-specific considerations should be taken into account.

**Keywords:** species richness, abundance, oldfield, reptile, plywood cover board, metal cover board

### Introduction

Throughout Ohio's history, its landscape has experienced dramatic shifts in the amount of cover by grassland habitat. Prior to European settlement, grasslands were rare, covering only 2.5% of the state. This steadily increased post-settlement with conversion of forest to agriculture, and has been declining over the last 50 years (Ohio Division of Wildlife, 2015). An estimated seven million acres of agricultural land has been lost across Ohio since 1950, with conversion to urban landscape being the primary cause since the 1990s (Western Reserve Land Conservancy, 2020). Subsequently, species dependent on this early successional habitat have been experiencing declines, with grassland birds being some of the most severely impacted taxa (Brennan and Kuvlesky, 2005). In response, grassland restoration practices have become common, generally with the goals of increasing plant diversity and improving habitat for wildlife. To achieve vegetation diversity, counteract forest succession, and control invasive and weedy species, a variety of management techniques have been used (e.g., controlled burns, mowing/haying, grazing, and herbicides), all which can have variable direct and indirect effects on native fauna. For taxa with limited dispersal capabilities (such as snakes), management strategies such as mowing and fire can cause direct mortality (Durbian, 2006), but it is suggested that the overall rate is low (Russell et al., 1999). Negative indirect effects can also occur in the short term, leading to unsuitable microhabitat (McLeod and Gates, 1998; Durbian, 2006) and predation risk (Durbian, 2006). However, some studies suggest that management may benefit snake populations or have no detectable effect. For example,

smooth snake (*Coronella austriaca*) densities were similar between sites receiving brush management (mowing and tree/bush cutting) versus no management (Graitson et al., 2020), and Oklahoma pastures receiving fire combined with herbicide treatments resulted in higher snake abundance when compared to unmanaged control sites (Jones et al., 2000). Although some management strategies may have minimal negative short-term impacts, the long-term effects of maintaining early successional habitat likely outweigh these consequences as forest encroachment leads to species replacement.

Early successional habitat can be critical for the persistence of some snake species (Fitch, 2006a; Steen et al., 2015; Diaz and Blouin-Demers, 2017), but few studies have addressed how succession of unmanaged grasslands impacts snake communities. In northern latitudes, small colubrid snakes are found in higher abundance in old fields than forests because old fields support their thermal requirements (Diaz and Blouin-Demers, 2017). A long-term study in Kansas suggested that as grasslands progress in successional age, there is a general trend for both increased abundance and species diversity until forest communities take over (Fitch, 2006b). However, these responses can be species-specific, and environmental factors may play an overarching role in their population dynamics (Fitch, 2006b). As agricultural lands are abandoned, these early successional areas could serve as important habitat for snakes. As reptiles face global declines (Gibbons et al., 2000; Reading et al., 2010), understanding the responses of these taxa to management and restoration strategies versus unmanaged succession is important for successful conservation. The goal of this study was to assess how successional age of unmanaged grasslands and cover board type impact snake community composition (species abundance and richness). Plywood and corrugated metal cover boards were used in combination to maximize sampling effort and to determine species-specific preferences, as there is controversy in the literature as to which type of artificial cover is most effective for sampling snakes. Further, we addressed whether community composition differed between morning and evening surveys (during one of the sampling years), as evening sampling is rarely reported in the literature. Surveys were conducted over four summers at the James H. Barrow Biological Field Station (JHBBFS; Hiram College, Portage County, OH, USA) in grasslands of young (4–7 years), mid-successional (12–15 years), and old (>50 years) successional age. We expected that the relative abundance and species richness of snakes would increase with successional age. Regardless of site, we predicted that snake diversity would increase from year one of the study to year four, as the boards became established at these sites. Further, we hypothesized that snake diversity would be higher during morning sampling efforts than in the evening due to morning thermoregulation behaviors.

## Methods

**Study Sites.** Hiram College's James H. Barrow Biological Field Station (Portage County, OH, USA, 41°29'90" N, 81°10'91" W) covers approximately 500 acres and includes a mixture of un-timbered, old-growth beech-maple forest, transitional second-growth forest, successional (unmanaged) and managed grasslands, wetlands and streams. While approximately 350 acres is contiguous, the Eagle Creek Restoration Site property (152 acres) is separated from the rest of the field station property by a state route and small residential property. Two of the grasslands chosen for this study (Black Walnut Grove and Stavenger Field) occur on the main portion of the field station property, while the third occurs on the Eagle Creek Restoration Site property (Eagle Creek Grassland).

Each grassland site was selected for surveys based on age when agriculture and subsequent years of mowing ceased or when the grassland was created and seeded, all remaining unmanaged since. Black Walnut Grove represents the oldest successional age (>50 years); Stavenger Field represents mid-successional age (12–15 years), and Eagle Creek Grassland represents the youngest successional age (4–7 years). The Eagle Creek Grassland was created from substrate excavated from a stream restoration project on the property and seeded with a native prairie mix purchased from Ohio Prairie Nursery (Portage County, Ohio, USA) four years prior to this study. While *Solidago* spp. was the dominant vegetation at all sites, the following vegetation was also abundant: *Rosa multiflora* (youngest and oldest successional sites), *Rubus* spp. (youngest and oldest successional sites), *Eryngium yuccifolium* (youngest successional site), and *Aster vimineus* (mid-successional site).

**Transect Design and Snake Surveys.** A combination of 10 corrugated metal (tin roofing material) and 10 half-inch plywood cover boards (all 1 m<sup>2</sup>) were placed at each site during early May 2016 (a total of 20 at each site; 60 total cover boards). At each site, cover boards were arranged in two parallel transects (10 boards per transect) spaced two meters apart horizontally and five meters apart along the length of the transect. Placement of cover boards was randomly assigned to ensure 10 cover boards of each type were in each transect and that metal and plywood cover boards were not directly next to each other in their horizontal orientation.

Snake surveys were conducted once a week during the summers of 2016 through 2019 covering a 12-week time period beginning the first week of June and ending in August for each year. All sites were surveyed on a single day during the hours of 8:30–10:30 a.m. and the order in which they were surveyed was randomly selected. They were conducted on days with

partial to full sun and no rain during the time of survey. To survey snakes, each board was lifted, and snakes were captured by hand. Each individual was identified to species and measured for snout-to-vent length (cm) using a standard measuring tape. All snakes were released back under the cover board under which they were found. All uncaptured snakes (6%) were able to be identified to species.

To compare species diversity during morning versus evening, surveys were conducted from 22 June 2016 to 30 September 2016 following the same procedure and using the same study sites and transect design. Evening surveys took place during the hours of 6:30–8:30 p.m. once each week and were done on different days of the week than morning surveys to minimize snake disturbance.

**Statistical Analysis.** A total of 172 eastern milk snakes, 85 northern brown snakes, and 419 eastern garter snakes were included in analyses. northern red-bellied snakes were excluded from analyses because only three were collected, and these only in the first year of sampling. Repeated captures were removed from analyses and were based on length and distinguishable markings (i.e., developmental abnormalities or injuries). Generalized linear mixed-effect models (GLMMs) using R package “lme4” (version 1.1.21; Bates et al., 2015) were used to determine whether cover board type (metal versus plywood), year (2016, 2017, 2018, 2019), or site type (youngest, mid-, and oldest successional age) influenced snake abundance and species richness. Board number was selected as a nested effect due to having repeated measures within a single site and a Poisson distribution was chosen for our inclusion of count data. A Tukey-Kramer post-hoc test was used to determine site-by-year interactions on snake abundance and species richness. To assess the effect of morning and evening sampling in 2016, separate GLMMs were used to determine differences in snake abundance and species richness, selecting site type, cover board type, and time of day as factors in the model. This model was constructed with board number as a random factor and a Poisson distribution was chosen for our inclusion of count data. A Tukey-Kramer post-hoc test was used to determine the time of day by cover board type interaction on snake abundance and species richness. To assess seasonal peaks from 2016 through 2019, we used a separate GLMM to determine if the week over the season influenced snake abundance. This model was constructed with board number as a random factor and a Poisson distribution was chosen for our inclusion of count data.

**Species-Specific Differences.** To determine the potential association between each snake species and cover board type, separate chi-square tests of independence were used for each species. Data were pooled across years to determine differences in overall species abundance across sites. A one-way ANOVA was also used to determine species-specific associations with successional age, testing the difference between the abundance of each species of snake captured and site type, followed by a Tukey-Kramer post-hoc test to determine species by site interactions. All analyses were conducted in R version 3.4.1 (R Core Team, 2019).

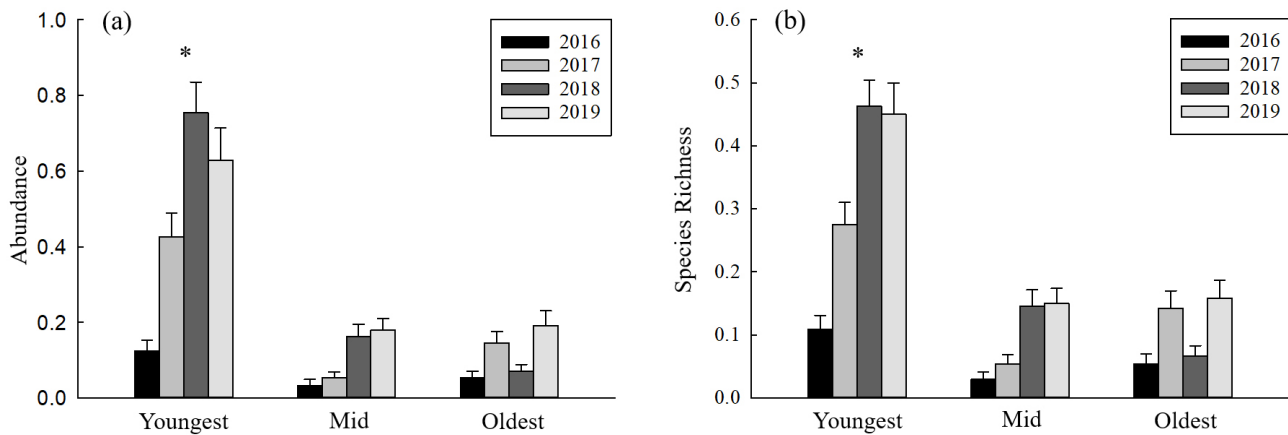
## Results

**Snake Abundance and Species Richness.** A total of 679 snakes (including recaptures) were recorded, representing four different species across all sites and years: 419 eastern garter snakes (*Thamnophis sirtalis sirtalis*, snout-vent-length [SVL] range = 13.0–93.7 cm), 85 northern brown snakes (*Storeria dekayi dekayi*, SVL range = 14.5–39.0 cm), 172 eastern milk snakes (*Lampropeltis triangulum*, SVL range = 22.0–98.2 cm), and 3 northern red-bellied snakes (*Storeria occipitomaculata occipitomaculata*, SVL range = 15.1–22.2 cm). Northern red-bellied snakes were captured in the mid- (two individuals) and old (one individual) successional sites, but not in the youngest site and only during the first year of survey. During the first year of capture (2016), 43 and 45 snakes were captured during morning and evening sampling, respectively.

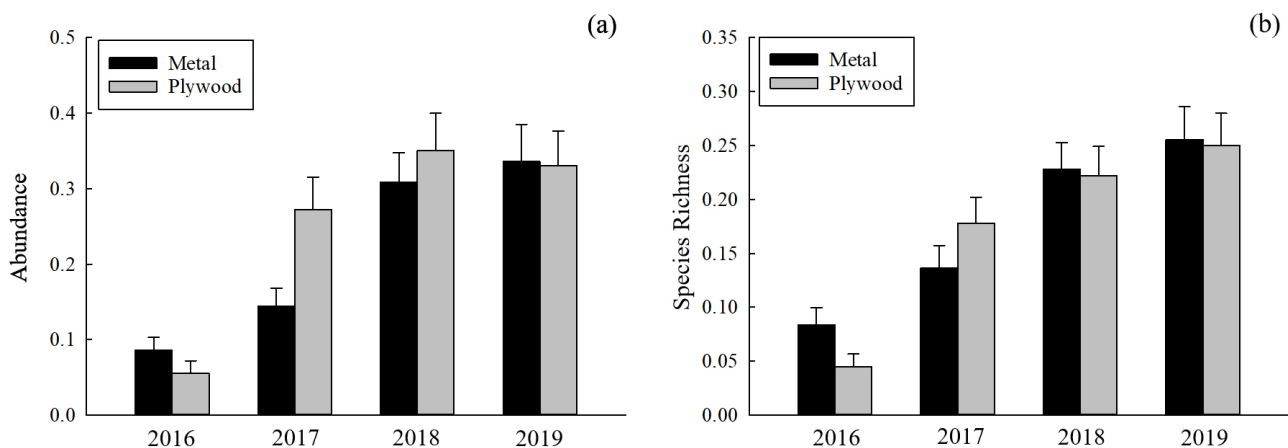
Both snake abundance and species richness varied across sampling years and site types. Regardless of year, the youngest successional site had significantly higher snake abundance (GLMM,  $p < 0.001$ ; Fig. 1a) and species richness (GLMM, both  $p < 0.001$ ; Fig. 1b) than both the mid- and oldest successional sites. Overall, species abundance was lowest in 2016 (GLMM,  $p < 0.001$ ; Fig. 1a), followed by 2017, (GLMM,  $p < 0.001$ ; Fig. 1a), while 2018 and 2019 did not differ in species abundance (GLMM,  $p > 0.05$ ; Fig. 1a). Similarly, species richness was significantly lower in 2016 than any other sampling year (GLMM,  $p < 0.001$ ; Fig. 1b), and 2017 had significantly lower species richness than 2018 (GLMM,  $p = 0.023$ ; Fig. 1b) and 2019 (GLMM,  $p < 0.001$ ; Fig. 1b). Snake abundance (GLMM,  $p < 0.001$ ; Fig. 1a) was significantly lower at the youngest successional site in 2016 than all other sampling years. Species richness was significantly lower in 2016 for the youngest successional site than in 2017 (GLMM,  $p < 0.001$ ; Fig. 1b). However, no significant differences in abundance (GLMM,  $p = 0.58$ ; Fig. 1a) or species richness (GLMM,  $p = 0.71$ ; Fig. 1b) occurred across all four sampling years for the mid-successional and oldest successional sites. Regardless of site type and year of survey, cover board type (metal versus plywood) did not have a significant effect on either snake abundance (GLMM,  $p = 0.43$ ; Fig. 2a) or species richness (GLMM,  $p = 0.33$ ; Fig. 2b). Further, neither snake abundance (GLMM,  $p = 0.83$ ; Fig. 3a) nor species richness (GLMM,  $p = 0.99$ ; Fig. 3b) varied based on time of day (morning versus evening surveys). However, in 2016, significantly more snakes and higher species richness were detected under plywood

than metal cover boards (GLMM,  $p=0.024$ , and  $p=0.013$ , respectively; Fig 3a, b). Additionally, there was no effect of week on snake abundance or species richness over the four years (GLMM,  $p>0.05$ ).

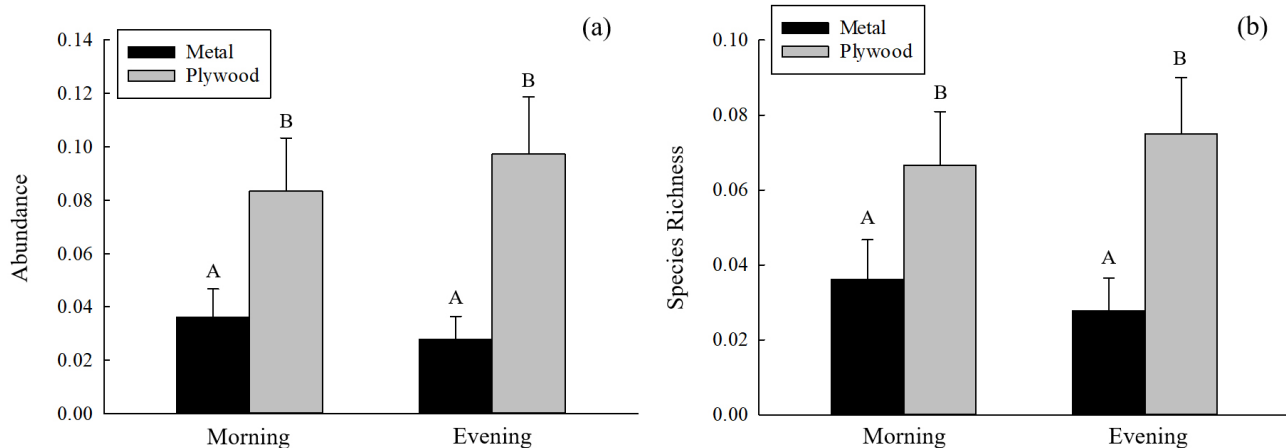
**Species-Specific Differences.** No association was detected between snake abundance and cover board type for any of the three main species captured (eastern garter snake, northern brown snake, and eastern milk snake; chi-square test,  $\chi^2(4)=6$ ,  $p=0.19$ ). However, there was a significant effect of successional site age on species-specific abundance (ANOVA,  $F_{8,8631}=73.56$ ,  $p<0.001$ ; Fig. 4a-c). Significantly more eastern garter snakes than northern brown snakes were captured at the youngest successional site (ANOVA,  $p<0.001$ ). Additionally, eastern garter snake abundance was higher at the youngest successional site than either the mid- or oldest successional sites (ANOVA, both  $p<0.001$ ; Fig. 4a). The youngest successional site also had a higher abundance of eastern garter snakes compared to eastern milk snakes (ANOVA,  $p<0.001$ ; Fig. 4a and c), and abundance of eastern milk snakes was significantly higher at the youngest successional site compared to the oldest successional site (ANOVA,  $p=0.035$ ; Fig. 4c). All other comparisons of species abundance across sites were not significant (ANOVA, all  $p>0.05$ ).



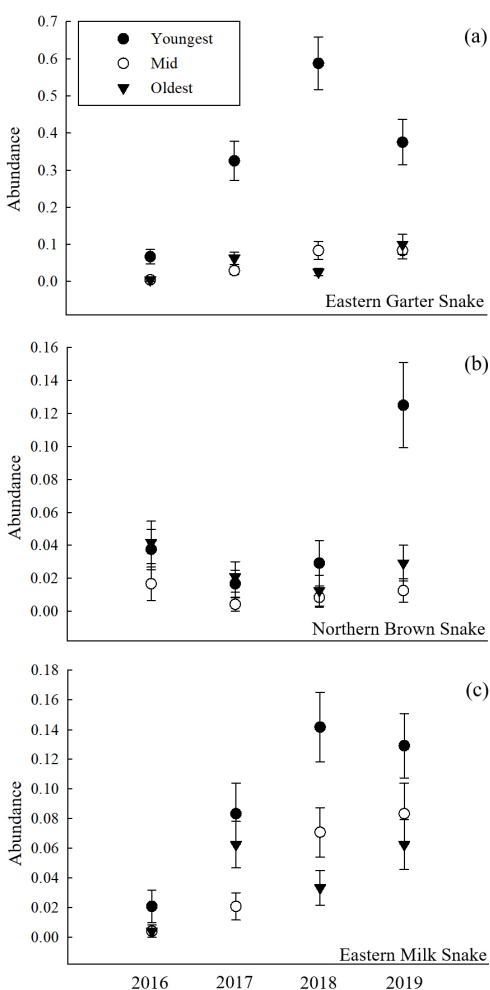
**Figure 1.** Average snake abundance (a) and species richness (b) (mean  $\pm$  1 SE) across all four survey years for each site type. Data are pooled across cover board type. Black bars = 2016, dark gray bars = 2017, charcoal bars = 2018, light gray bars = 2019. The asterisk indicates a significant difference by site type.



**Figure 2.** Average snake abundance (a) and species richness (b) (mean  $\pm$  1 SE) across all four survey years for each board type. Data are pooled across site type. Black bars represent corrugated metal cover boards and gray bars represent plywood cover boards.



**Figure 3.** Average snake abundance (a) and species richness (b) (mean  $\pm$  1 SE) during morning and evening surveys for summer 2016 for each board type. Data are pooled across all three sites. Black bars represent corrugated metal cover boards and gray bars represent plywood cover boards. Letters above SE bars indicate post-hoc Tukey-Kramer results.



**Figure 4.** Average snake abundance (mean  $\pm$  1 SE) for eastern garter snake (a), northern brown snake (b) and eastern milk snake across each survey year. Data are pooled across board type. Black circles = youngest successional site, white circles = mid-successional site, black upside-down triangles = oldest successional site.

## Discussion

Across four years of survey, both snake species abundance and richness was highest in the youngest successional site. Both the mid- and old successional sites yielded similar diversity, suggesting that abundance and species richness may peak before 12 years of grassland successional age. Since snakes were not marked, we are unable to be certain that individuals were not recaptured during surveys. However, snakes that had the same body length were excluded from analysis, and our results should reflect comparative differences in abundance across sites. These results are supported by a long-term study in Kansas in which ceasing of grazing and cultivation led to increased abundance of the majority of herpetofauna initially, with declines occurring over time as the forest community encroached (Fitch, 2006a). For small colubrid snakes like common garter snakes and red-bellied snakes, open oldfields are preferred over forested habitats as they offer more favorable thermal conditions (Diaz and Blouin-Demers, 2017), further suggesting that as grasslands age, snake species relying on this habitat are negatively affected.

In the youngest successional site, both abundance and species richness increased from year one of the study, peaked at year three, and then remained similar across years three and four, suggesting that populations may have been establishing in this early successional site. Since abundance and species richness remained similar for the mid- and old successional sites across the four-year study, it is unlikely that length of time that cover boards were present played a role in detection of snakes and further supports that there is likely a threshold reached in snake diversity that correlates to successional age. Supporting this, another study suggested that newly placed cover boards take only two months to reach peak efficiency (Grant et al., 1992). Responses to successional age were species-specific, both in this study and those conducted by Fitch (2006a, 2006b). In this study, eastern garter snakes and eastern milk snakes were the most common species detected. Although eastern garter snakes were in highest abundance at the youngest successional site, eastern milk snakes were found in similar abundance in the young and mid-successional sites. Similarly, Fitch (2006a) reported that eastern



milk snakes increased for more than a decade and then declined with successional age. In contrast to our study, Fitch (2006b) reported that eastern garter snakes did not undergo drastic declines like the other snake species in their study and showed fluctuations in occurrence over time. The close proximity of our young successional site to aquatic habitats may be driving this pattern, as this species feeds largely on aquatic prey (Fitch, 2006a). However, northern brown snakes were found in similar abundance across all three sites, suggesting that either successional age did not drive their habitat use, or (because they were detected in low numbers overall) changes in population may not be able to be observed. This same pattern was observed in this species by Fitch (2006b), which also had very low numbers of occurrences and suggested that population changes could not be determined due to low sample size. This species, in particular, is cryptic and difficult to capture due to its fossorial behavior. northern red-bellied snakes were only detected during one year of sampling, with very few individuals captured. Surveys conducted at JHBBFS between 2001 and 2004 also captured all four of these species and, similar to our study, found eastern garter snakes in high abundance (Meshaka et al., 2008). However, in contrast, they found northern brown snakes in high abundance and eastern milk snakes were detected in substantially lower numbers than the former two species (Meshaka et al., 2008). Also, similar to our results, red-bellied snakes were present, but in low numbers compared to the other three species (Meshaka et al., 2008). Because individuals were not tracked in our study, it is difficult to determine whether northern brown snakes have declined and eastern milk snakes have increased over time. Further, Meshaka et al. (2008) detected seasonal peaks by age class, which was not observed in our study due to low numbers of juveniles. Additionally, Meshaka (2010) detected species-specific seasonal peaks in occurrence under cover boards during certain times in summer with similar species in Pennsylvania, and these seasonal peaks were not observed in our study.

A variety of abiotic and biotic mechanisms are likely driving these patterns and may be strongly correlated with successional age. For herpetofauna in general, thermoregulatory requirements are among the main factors impacting habitat selection because much of their physiology and behavior is dependent on temperature (Huey, 1991; Lelièvre et al., 2011), especially for snakes in cold climates and temperate zones (Lourdais et al., 2013). Since range in thermal requirements is species-specific, some thrive in open habitats while others can tolerate habitats with a wider thermal regime (Lelièvre et al., 2011). Additionally, the availability of cover objects, both artificial and natural, likely has a strong impact on habitat selection because they offer snakes protection from predation as well as potentially favorable hydric and thermal microhabitats (Grant et al., 1992; Hampton, 2007; Lelièvre et al., 2010). In this study, neither species-specific nor community responses indicated preference for plywood or metal cover boards, with the exception of the first year of study, when comparisons were made across morning and evening surveys and surveys extended into September. During that first year, both abundance and species richness were highest under plywood cover boards but did not differ for time of day, suggesting that seasonality may play a role in board preference type, as no board preference was detected during morning-only surveys from June through August. This contradicts other studies that show preferences by reptiles for tin cover objects over plywood (Grant et al., 1992; Hampton, 2007). Other studies suggest that responses can be species-specific—e.g., red-bellied snakes can show a preference for tin (Halliday and Blouin-Demers, 2015; Diaz and Blouin-Demers, 2017), while garter snakes have conflicting preferences in the literature (Englestoft and Ovaska, 2000; Diaz and Blouin-Demers, 2017)—but no species-specific preferences were observed in this study.

Although the majority of studies survey snakes in the morning, our results suggest that evening surveys could produce a similar outcome for population and community studies. Grant et al. (1992) found time-of-day surveys to be site-specific, also making concessions that a variety of factors could influence whether or not time of day had any impact on the community assemblage.

Although temperature and cover objects are often accepted as the driving mechanisms for habitat selection, factors including but not limited to environmental moisture (Fitch, 2006b), food availability (Huey, 1991; Fitch, 2006b), predation risk (Webb and Whiting, 2005), vegetation cover (Pringle et al., 2003), and interspecific competition (Luiselli, 2006) can impact habitat use by snakes at both the individual and species level and are likely not mutually exclusive. For example, Fitch (2006b) suggested that low moisture in drought years negatively impacted the availability of earthworms (a major food source for young-of-year red-sided garter snakes), leading to low survivorship and possibly delayed maturity (Fitch, 2006b). Further, snake declines were detected in species specializing on small rodents (e.g., voles), which correlated with vole declines associated with increased grassland successional age (Fitch, 2006a). In our study, up to nine individuals were captured under a single board, and it was not uncommon to find eastern garter snakes, northern brown snakes, and eastern milk snakes sharing boards. Of particular interest, snakes appeared to avoid boards in which ants developed colonies, suggesting that a variety of factors impact habitat use by snakes and microhabitat-level constraints are important to consider.

Many studies have linked landscape-level factors such as surrounding land use type (Cagle, 2008), distance from habitat edge (Cagle, 2008), and habitat fragmentation (Breininger et al., 2012) to snake occurrence, but responses are often species-specific. Further, roads also fragment landscapes and associated snake mortalities are also a known risk for populations (Breininger et al., 2012; Jochimsen et al., 2014). In this study, landscape features could impact source populations, mobility, and dispersal as a mix of forest, agriculture, and residential areas all occur within a kilometer of each survey site. Patch size can also be an

important driver of snake community composition, with larger patches having highest abundance and species richness (Kjoss and Litvaitis, 2001). However, this was likely not a factor in this study, as the mid-successional site was the largest grassland patch and the youngest and oldest sites were both relatively small and of similar size.

Although there is limited published literature describing the effects of successional age of unmanaged grasslands on snake assemblages, it is generally understood that open and early successional habitats are important for snake populations. Habitat loss is a major factor in the decline of snake populations (Gibbons et al., 2000), and with grasslands being the most endangered ecosystem in North America (Samson et al., 2004), more attention should be focused on taxa that are reliant on these habitats. Population declines are particularly evident in areas with dwindling habitat such as Midwest tallgrass prairies (Cagle, 2008). Management of grasslands to prevent encroachment of woody vegetation is likely necessary to provide this critical open habitat for some species (Lagory et al., 2009). However, several studies have suggested that these practices should be timed with periods when snakes are inactive to minimize mortality, and that management strategies create high habitat heterogeneity to benefit multiple species. Because our results are limited to only one study area, generalized conclusions cannot be made and more studies should be conducted to look at general patterns of successional age on grassland snake assemblages, especially with comparison made in unmanaged versus managed sites using long-term surveys.

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### References Cited

- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(1): 1–48.
- Breiner, D.R., M.J. Mazerolle, M.R. Bolt, M.L. Legare, J.H. Drese, and J.E. Hines. 2012. Habitat fragmentation effects on annual survival of the federally protected eastern indigo snake. *Animal Conservation* 15: 361–368.
- Brennan, L.A., and W.P. Kuvlesky, Jr. 2005. North American grassland birds: an unfolding conservation crisis? *Journal of Wildlife Management* 69: 1–13.
- Cagle, N.L. 2008. Snake species distributions and temperate grasslands: a case study from the American tallgrass prairie. *Biological Conservation* 141: 744–755.
- Diaz, F.R., and G. Blouin-Demers. 2017. Northern snakes appear much more abundant in old fields than in forests. *The Canadian Field-Naturalist* 131: 228–234.
- Durbian, F.E. 2006. Effects of mowing and summer burning on the massasauga (*Sistrurus catenatus*). *The American Midland Naturalist* 155: 329–334.
- Engelstoft, C., and K.E. Ovaska. 2000. Artificial cover-objects as a method for sampling snakes (*Contia tenuis* and *Thamnophis* spp.) in British Columbia. *Northwestern Naturalist* 81: 35–43.
- Fitch, H.S. 2006a. Collapse of a fauna: reptiles and turtles of the University of Kansas Natural History Reservation. *Journal of Kansas Herpetology* 17: 10–13.
- Fitch, H.S. 2006b. Ecological succession on a natural area in northeastern Kansas from 1948 to 2006. *Herpetological Conservation and Biology*. 1: 1–5.
- Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Greene, T. Mills, Y. Leiden, S. Poppy, and C.T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50: 653–666.
- Graitson, E., S. Urnenbacher, and O. Lourdais. 2020. Snake conservation in anthropized landscapes: considering artificial habitats and questioning management of semi-natural habitats. *European Journal of Wildlife Research* 66: 39.
- Grant, B., A. Tucker, J. Lovich, A. Mills, P. Dixon, and J. Gibbons. 1992. The use of coverboards in estimating patterns of reptile and amphibian biodiversity, pp. 379–403. *In* D.R. McCullough, R.H. Barrett (eds.). *Wildlife 2001: Populations*. Springer, Dordrecht.
- Halliday, W., and G. Blouin-Demers. 2015. Efficacy of coverboards for sampling small northern snakes. *Herpetology Notes* 8: 309–314.
- Hampton, P. 2007. A comparison of the success of artificial cover types for capturing amphibians and reptiles. *Amphibia-Reptilia* 28: 433–437.
- Huey, R.B. 1991. Physiological consequences of habitat selection. *The American Naturalist* 137: S91–S115.
- Jochimsen, D.M., C.R. Peterson, and L.J. Harmon. 2014. Influence of ecology and landscape on snake road mortality in a

- sagebrush–steppe ecosystem. *Animal Conservation* 17: 583–592.
- Jones, B., S.F. Fox, D.M. Leslie, Jr., D.M. Engle, and R.L. Lochmiller. 2000.** Herpetofaunal responses to brush management with herbicide and fire. *Journal of Range Management* 53: 154–158.
- Kjoss, V.A., and J.A. Litvaitis. 2001.** Community structure of snakes in a human-dominated landscape. *Biological Conservation* 98: 285–292.
- Lagory, K.E., L.J. Walston, C. Goulet, R.A. Van Lonkhuyzen, S. Najjar, and C. Andrews. 2009.** An examination of scale-dependent resource use by eastern hognose snakes in southcentral New Hampshire. *Journal of Wildlife Management* 73: 1387–1393.
- Lelièvre, H., G. Blouin-Demers, X. Bonnet, and O. Lourdais. 2010.** Thermal benefits of artificial shelters in snakes: a radiotelemetric study of two sympatric colubrids. *Journal of Thermal Biology* 35: 324–331.
- Lelièvre, H., G. Blouin-Demers, D. Pinaud, H. Lisse, X. Bonnet, and O. Lourdais. 2011.** Contrasted thermal preferences translate into divergences in habitat use and realized performance in two sympatric snakes. *Journal of Zoology* 284: 265–275.
- Lourdais, O., M. Guillon, D. DeNardo, G. Blouin-Demers. 2013.** Cold climate specialization: adaptive covariation between metabolic rate and thermoregulation in pregnant vipers. *Physiology and Behavior* 119: 149–155.
- Luiselli, L. 2006.** Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. *Oikos* 114: 193–211.
- McLeod, R.F., and J.E. Gates. 1998.** Response of herpetofaunal communities to forest cutting and burning at Chesapeake Farms, Maryland. *The American Midland Naturalist* 139: 164–177.
- Meshaka, Jr., W.E. 2010.** Seasonal activity and breeding seasons of snakes from Powdermill Nature Reserve in Western Pennsylvania. *Herpetological Conservation and Biology* 51: 155–165.
- Meshaka, Jr., W.E., S.D. Marshall, and T.J. Guiher. 2008.** Seasonal activity and reproductive characteristics of an oldfield grassland snake assemblage: Implications for land management. *Herpetological Bulletin* 105: 35–40.
- Ohio Division of Wildlife. 2015.** Ohio’s State Wildlife Action Plan. Columbus, Ohio, USA.
- Pringle, R.M., J.K. Webb, and R. Shine. 2003.** Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* 84: 2668–2679.
- R Core Team. 2019.** R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Reading, C.J., L.M. Luiselli, G.C. Akani, X. Bonnet, G. Amori, J.M. Ballouard, E. Filippi, G. Naulleau, D. Pearson, and L. Rugiero. 2010.** Are snake populations in widespread decline? *Biology Letters* 6: 777–780.
- Russell, K.R., D.H. Van Lear, and D.C. Guynn, Jr. 1999.** Prescribed fire effects on herpetofauna: review and management implications. *Wildlife Society Bulletin* 27: 374–384.
- Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004.** Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* 32: 6–15.
- Steen, D.A. P.A. Osborne, M. Dovčiak, D.A. Patrick, and J.P. Gibbs. 2015.** A preliminary investigation into the short-term effects of a prescribed fire on habitat quality for a snake assemblage. *Herpetological Conservation and Biology* 10: 263–272.
- Webb, J.K., and M.J. Whiting. 2005.** Why don’t small snakes bask? Juvenile broad-headed snakes trade thermal benefits for safety. *Oikos* 110: 515–522.
- Western Reserve Land Conservancy. 2020.** Farmland preservation. <https://www.wrlandconservancy.org/whatwedo/workingfarms/> (accessed 5 May 2020).