Grassland snake assemblages in central and western Pennsylvania and northeastern Ohio, USA

WALTER E. MESHAKA, JR.[1,5], SAMUEL D. MARSHALL[2], TIMOTHY J. GUIHER[3] and LINDSAY ZEMBA[4]

[1] *Section of Zoology and Botany, State Museum of Pennsylvania, 300 North Street, Harrisburg, PA 17120, USA*

[2] *Department of Biology, Northwestern State University, Natchitoches, LA 71497, USA*

[3] *College of Staten Island, CUNY, Department of Biology, Staten Island, NY 10314, USA*

[4] *Staff Biologist, ARM Group Inc., 1129 West Governor Road, P.O. Box 797 Hershey, PA 17033, USA*

[5] Corresponding author: wmeshaka@state.pa.us

ABSTRACT - Surveys of snake assemblages during 2001-2009 from 15 grasslands in central and western Pennsylvania and northeastern Ohio found that in smaller sites (4.6 ha) the Common Garter Snake (*Thamnophis sirtalis*) was nearly always the dominant snake out of as many as eight species found under cover boards, and generally followed by smaller, fossorial species that were considerably less abundant. At the single large site (101 ha), large individuals (> 105 cm SVL) of the Midland Rat Snake (*Scotophis spiloides*) and the Eastern Racer (*Coluber constrictor*) greatly outnumbered other species and no Common Garter Snakes were captured. Although not confirmed, the small size and isolated nature of the smaller grassland sites may have been the reason for the absence of the Eastern Racer. However, in domino effect, the absence of this large-bodied ophiophage may have allowed the Common Garter Snake to dominate, which in turn may have been a superior competitor for earthworms and also a possible predator of its competitors. Habitat structure of these sites appeared to be responsible for the status of some of the species as well as non-competitive, larger species at these sites. Thus, whereas conservation of the Eastern Racer is tied, in part, to large parcels of early successional grasslands, somewhat predictable responses by northeastern grassland snakes to successional changes within the grassland must also be taken into account when formulating conservation plans for disappearing habitat in the northeastern United States.

GRASSLANDS in the eastern United States have declined by 80% since the mid-1800s (Brennan & Kuvlesky, 2005). In the Northeast, succession of grasslands to forest has been the main source of grassland loss (Brennan & Kuvlesky, 2005). In a review of Pennsylvania grassland habitats, Duncan (2005) noted the occurrence of grasslands in Pennsylvania since the glacial retreat 11,000 years ago. These post-glacial grasslands were maintained by large herbivores, burning by Native Americans, and more recently by land clearing by European settlers. Land clearing associated with European settlement reduced forest cover to approximately 25% of its pre-Columbian coverage. In the last 200 years succession of agricultural land back to eastern deciduous forest has resulted in a net loss of previously predominant grassland habitats. Presently, approximately 25% of Pennsylvania's habitats are open. In neighboring Ohio, only 0.5% of the original 2,591 km^2 native tallgrass prairie remains and secondary grassland habitat, such as pastures and hayfields have declined 61% and 46% respectively, since 1950 (Swanson, 1996).

Recent interest has focused on secondary (i.e., anthropogenic) grasslands for conservation efforts. For example, the importance of large tracts has been shown to be important for a variety of grassland birds (Davis, 2004), such as the Grasshopper

Sparrow (Balent & Norment, 2003) and Henslow's Sparrows (Bajema & Lima, 2001). Research has revealed that small grasslands can become a sink for grassland species populations (Balent & Norment, 2003) or may be avoided altogether (Peterjohn, 2006). Community structure and dynamics of Midwestern grassland herpetofaunal communities have received attention (e.g., Fitch, 1999; Cavitt, 2000; Wilgers & Horne, 2006) as well as the loss of grassland habitat to succession (e.g., Fitch, 1999, 2005, 2006). Significantly, grassland habitats, whether primary or secondary, were found to have supported larger and more diverse herpetofaunal assemblages than forest habitats. In the northeast, less attention has been devoted to grassland herpetofaunas and often only in association with multi-habitat surveys of an area (e.g., Yahner et al., 2001; Tiebout III, 2003; Brotherton et al., 2005). However, a study in Connecticut that examined snake assemblages in relation to patch size found an effect of patch size on assemblage diversity and body size of snakes (Kjoss & Litvaitis, 2001).

The importance of rare and shrinking grassland habitats in Pennsylvania is evident in 37 vertebrate species identified by the Pennsylvania Wildlife Action Plan as worthy of conservation efforts (Duncan, 2005). Among terrestrial invertebrates in south-central Pennsylvania, butterflies were found to be more numerous in open habitat than in forest (Keller & Yahner, 2002). Appearing effectively as islands in an ocean of forest, grasslands provide us with an opportunity to examine responses of snakes to this habitat as well as responses to the assemblage structure to patch size of these grasslands at sites in Pennsylvania and northeastern Ohio.

METHODS AND MATERIALS

Powdermill Nature Reserve (PNR)

This 856.2 ha reserve is privately owned and operated by the Carnegie Museum of Natural History and is located in Rector, Westmoreland County, Pennsylvania, USA. Founded in 1957, tracts which had been farmed were allowed to reforest such that today 89.5 % of PNR is covered in mixed forest. Once each month we visited up to eight sites during May-September 2003-2009, depending on the site. Exceptionally, in 2003 visits did not commence until June instead of May. Cover boards were constructed of 1 x 3 m corrugated galvanized steel.

1. Crisp Meadow is a 1.0 ha site of mixed rangeland located near the station's bird-banding lab. It is convex in topography and is mowed each fall. Eight cover boards encircled most of the field and were monitored during 2003-2009.
2. Barn is a 0.9 ha site of mixed rangeland located along Rt 381 and southwest of Powdermill Run. It is convex in topography and very wet on its eastern side. The Barn site is mown each fall. Three cover boards were monitored during 2003-2009.
3. Friedline Left Entrance is a 3.1 ha site of rolling mixed rangeland that borders Rt. 381 and is located north of the Pennsylvania Turnpike. This site is irregularly mown during the fall. Seven cover boards were monitored during 2004-2009.
4. Friedline Right Entrance is a 2.2 ha site of rolling mixed rangeland that borders Rt. 381 and is located north of the Pennsylvania Turnpike. This site is irregularly mown during the fall. Seven cover boards were monitored during 2008-2009.
5. Friedline Original is a 0.6 ha site of mixed rangeland on a slope found southeast of Rt. 381 and north of the Pennsylvania Turnpike. This site is irregularly mown during the fall. Six cover boards partially encircled the field and were monitored during 2003-2009.
6. Friedline Foundation is a 2.1 ha site of mixed rangeland on a slope found southeast of Rt. 381 and north of the Pennsylvania Turnpike. This site is irregularly mown during the fall. One cover board was monitored during 2008-2009.
7. Friedline Corners is a 14.6 ha site of rolling fallow field that is located along the corner of Rt. 381 and the Pennsylvania Turnpike. This site is irregularly mown during the fall. Three cover boards were monitored during 2006-2009.
8. Friedline Turnpike is a 4.9 ha site of a rolling fallow field that is located east of Rt. 381 and faces the Pennsylvania Turnpike. This site is irregularly mown during the fall. Eight cover boards were monitored during 2004-2005 and

subsequently one cover board was monitored during 2006-2009.

Fort Indiantown Gap National Guard Training Center (FITG)

This 7500 ha military training ground is located in Dauphin and Lebanon counties, Pennsylvania, USA. Established in 1931, approximately 101 ha of grassland have been set aside for the protection of the Eastern Regal Fritillary Butterfly (*Speyeria idalia idalia*) (Ferster et al., 2008). The grassland is maintained by periodic disturbance by tanks, or "iron bison" (Ferster et al., 2008). At opposite ends of FITG, a single 3 x 1 m corrugated galvanized steel was monitored in section B-12, and a mix of eight 1 x 1 m plywood boards and 3 x 1 m corrugated galvanized steel were monitored at section D-3 during May-September 2005. The data were combined for one area. Ferster et al. (2008) provided a map of FITG.

Wildwood Park (WP)

This 96.3 ha county park is located in Harrisburg, Dauphin County, Pennsylvania, USA. WP is an urban park isolated from other semi-natural habitats by highways. WP is centred around an artificial lake that comprises over 60 % of an otherwise heavily forested park of mixed deciduous trees. The single 0.4 ha grassland site was created by clearing forest for an aborted road and is situated on a gentle slope. This site is mown each fall. Six 1 x 1 m untreated plywood boards were monitored during May-September (2004-2007).

James H. Barrow Field Station (JHBFS)

This 121.4 ha reserve is privately owned and operated by Hiram College and is located in Hiram Township, Portage County, Ohio, USA Founded in 1960, JHBFS habitats range from various stages of oldfield succession to 67% forest coverage of a primarily Beech-Maple community. Monthly visits occurred at five sites during May-September (2001-2004). Exceptionally, boards were monitored daily for one week each September. Cover boards were constructed of 1 x 1 m untreated plywood. Ten cover boards were set 2 m apart from each other.

1. Front Road is a 1.6 ha early successional oldfield site that borders agricultural crop land. This site was monitored in 2004.
2. Mulch Pile is a 1.20 ha mid-successional oldfield site with scattered shrubs and small deciduous trees. This site was monitored during 2002-2004.
3. Oil Well is a 0.2 ha early successional Oldfield site that is surrounded by forest on 3 sides and by field on one side. This site was monitored during 2001-2004.
4. Old Field is a 2.8 ha mid-successional oldfield site that is scattered with shrubs and small deciduous trees. This site was monitored during 2001-2004.
5. Wet Site is a 1.3 ha late successional oldfield site. Shrubs and trees are extensive. The site borders a wetland and was monitored during 2001-2004.

At sites except JHBFS, snakes were captured, and immediately sexed, measured for snout-vent length (SVL) and either fitted with an AVID Passive Integrated Transponder (PIT) tag for individual recognition or a ventral scale clip to note that the animal was marked. Snakes were released immediately afterwards. At JHBFS, individual marking by use of AVID chips only, was restricted to a subset of snakes. For this reason, only total captures were examined for JHBFS. All other protocols were followed at JHBFS. Means are followed by + 2 standard deviations. Common names follow the arrangement by Collins & Taggart (2009).

RESULTS

Powdermill Nature Reserve

We recorded 1056 captures of 669 marked snakes of eight species at PNR during 2002-2007. For all sites, the Common Garter Snake (*Thamnophis sirtalis*) was the most abundant species accounting for 71.6% of all snake captures and 64.3% of all new snakes captured during the study (Fig. 1). The Redbelly Snake (*Storeria occipitomaculata*) was second in abundance for all sites as measured by all captures (11.6%) and all new snakes (17.2%), both of whose abundance values only slightly exceeded those of the Ringneck Snake (Fig. 1).

Overwhelming dominance of the Common Garter Snake on PNR grasslands was evident at

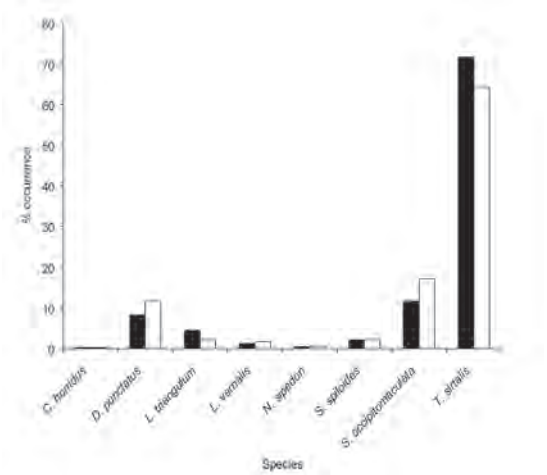

Figure 1. Relative abundance of snakes at all eight grassland sites combined from Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2003-2009. Solid bars denote the percent of all captures (n = 1056). Open bars denote the percent of all new captures (n = 669).

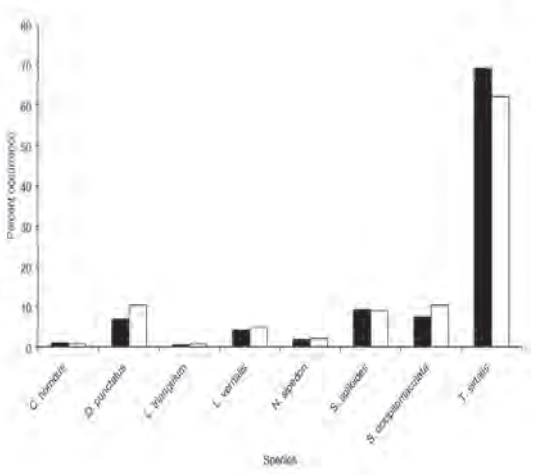

Figure 2. Relative abundance of snakes at the Crisp Meadow site at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2003-2009. Solid bars denote the percent of all captures (n = 217). Open bars denote the percent of all new captures (n = 145).

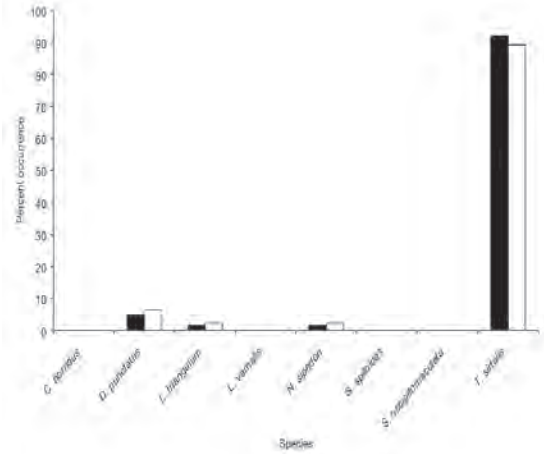

Figure 3. Relative abundance of snakes at the Barn site at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2003-2009. Solid bars denote the percent of all captures (n = 63). Open bars denote the percent of all new captures (n = 47).

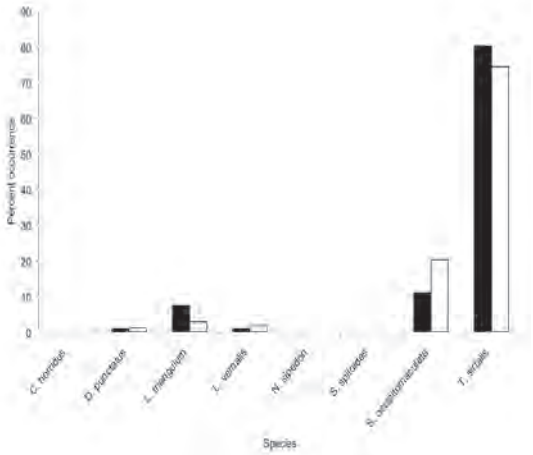

Figure 4. Relative abundance of snakes at the Friedline Left Entrance site at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2004-2009. Solid bars denote the percent of all captures (n = 367). Open bars denote the percent of all new captures (n = 183).

seven sites (Figs. 2-9) and similar to that of the Redbelly Snake at one site (Fig. 5). However, the distribution and composition varied greatly among the remaining species. Likewise, the overall abundance of snakes, as measured by numbers of snakes/cover board, varied extensively among sites (Fig. 10). Three species co-occurred at four sites (Figs. 5, 7, 8, 9), four species co-occurred at one site (Fig. 3), five species co-occurred at two sites (Figs. 4, 6), and eight species co-occurred at one site (Fig. 2). With one exception, Friedline Right Entrance (Fig. 5), snake species that co-occurred with the Common Garter Snake were generally much lower in abundance than the Common Garter

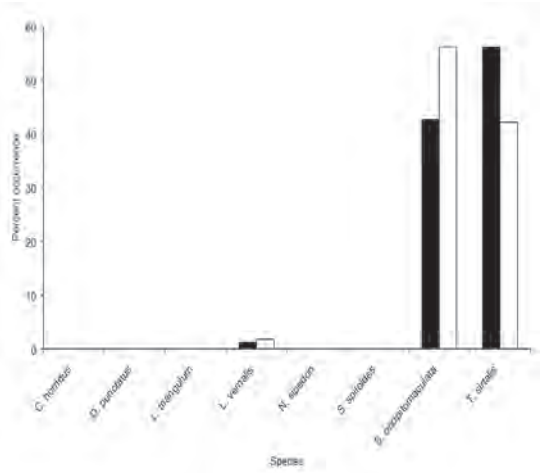

Figure 5. Relative abundance of snakes at the Friedline Right Entrance site at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2008-2009. Solid bars denote the percent of all captures (n = 82). Open bars denote the percent of all new captures (n = 57).

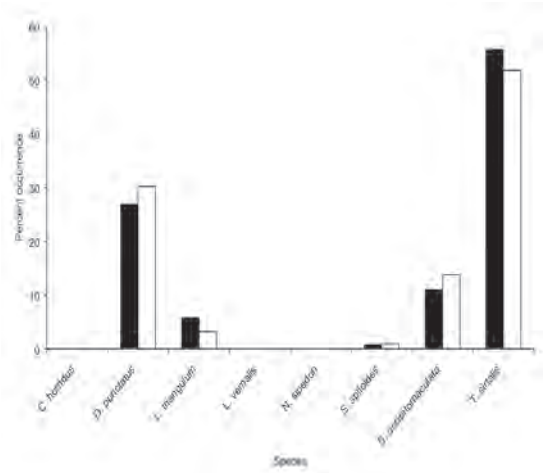

Figure 6. Relative abundance of snakes at the Friedline Original site at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2003-2009. Solid bars denote the percent of all captures (n = 246). Open bars denote the percent of all new captures (n = 189).

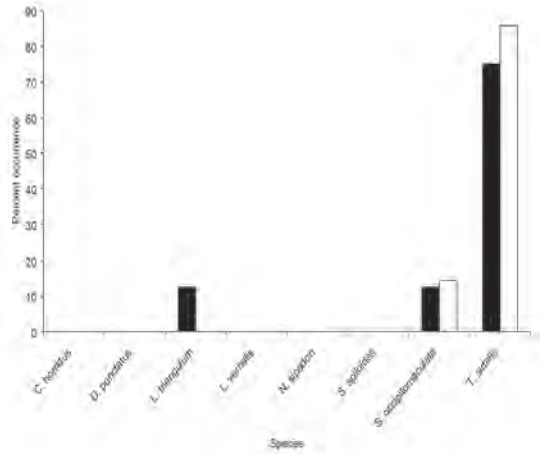

Figure 7. Relative abundance of snakes at the Friedline Foundation site at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2008-2009. Solid bars denote the percent of all captures (n = 8). Open bars denote the percent of all new captures (n = 7).

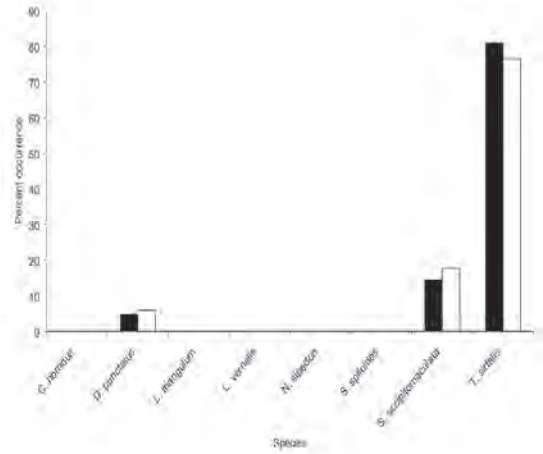

Figure 8. Relative abundance of snakes at the Friedline Corners site at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2006-2009. Solid bars denote the percent of all captures (n = 21). Open bars denote the percent of all new captures (n = 17).

Snake. The Ringneck Snake (*Diadophis punctatus*) or Redbelly Snake comprised the second most abundant snake at four sites (Figs. 3, 4, 6, 8). Along the edge of Crisp Meadow (Fig. 2), the Midland Rat Snake (*Scotophis spiloides*) was more numerous with respect to total number of captures than either the Ringneck Snake or Redbelly Snake. With a very small sample size, the Milk Snake and Redbelly Snake were similar in total Numbers of captures at Friedline Foundation (Fig. 7), and at Friedline Turnpike (Fig. 9) the Milk Snake (*Lampropeltis triangulum*) was more numerous in both total and new captures than was the Redbelly Snake. Number of snakes captured/cover board

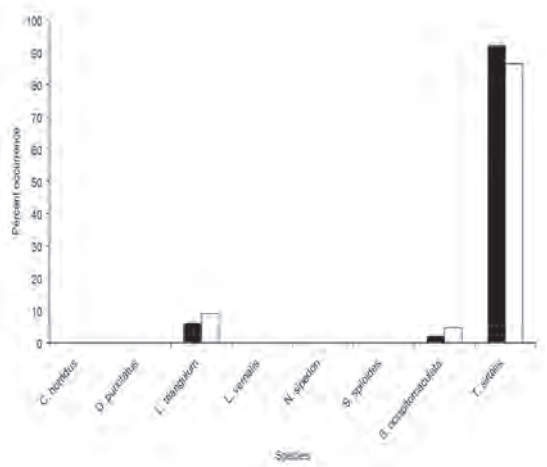

Figure 9. Relative abundance of snakes at the Friedline Turnpike site at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2006-2009. Solid bars denote the percent of all captures (n = 50). Open bars denote the percent of all new captures (n = 22).

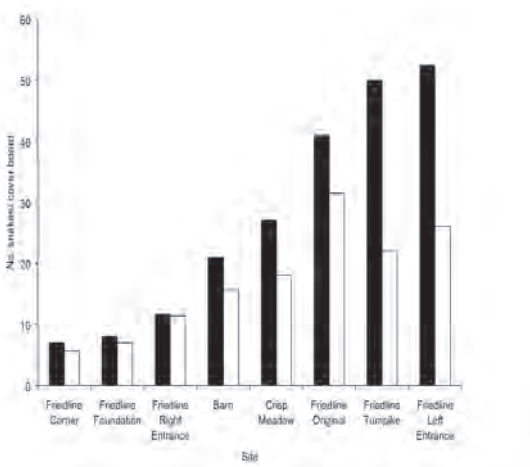

Figure 10. Number of snakes/ cover board at all eight grassland sites at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA, during 2003-2009. Solid bars denote the percent of all captures (n = 1056). Open bars denote the percent of all new captures (n = 669).

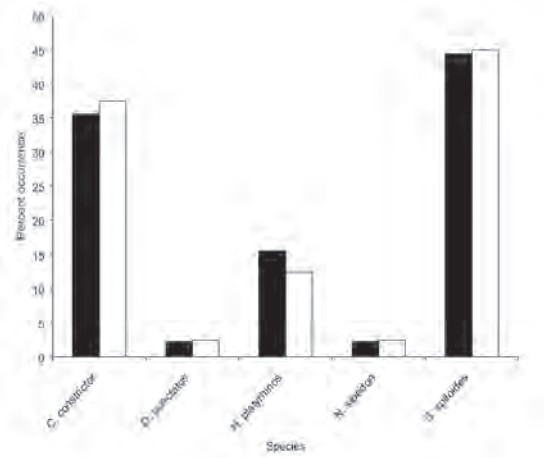

Figure 11. Relative abundance of snakes from grassland habitat at Fort Indiantown Gap National Guard Training Center, Dauphin and Lebanon counties, Pennsylvania, USA, in 2005. Solid bars denote the percent of all captures (n = 45). Open bars denote the percent of all new captures (n = 40).

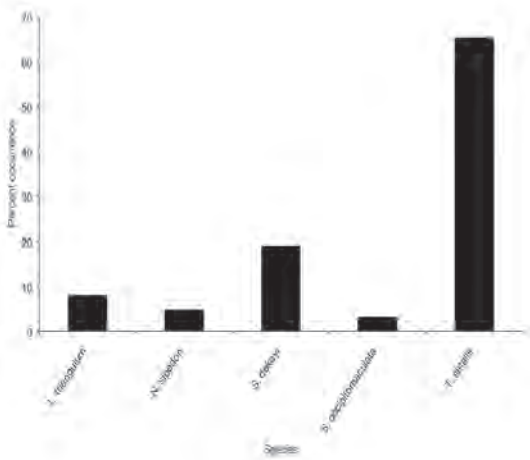

Figure 12. Relative abundance of snakes at all of the five grassland sites combined from the James H. Barrow Field Station, Portage County, Ohio, USA, during 2001-2004. Solid bars denote the percent of all captures (n = 566).

ranged 7.0-52.4 for total captures and 5.7-31.5 for new captures, the values of which appeared to have little to do with patch size (Fig. 10). No other reptilian species was captured under the cover boards. However, a trail that passes through Crisp Meadow was used as a nesting site by the Painted Turtle (*Chrysemys picta*), Wood Turtle (*Glyptemys insculpta*), and Box Turtle (*Terrapene carolina*). A hepetofaunal list recorded 21 amphibians and 18 reptiles for PNR (Meshaka et al., 2008a).

Fort Indiantown Gap Training Center

We recorded 45 total captures of 40 marked snakes of five species at FITG in 2005. Using

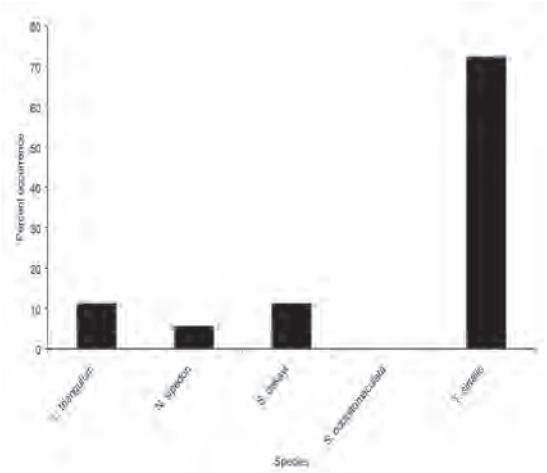

Figure 13. Relative abundance of snakes at the Front Road site at James H. Barrow Field Station, Portage County, Ohio, USA, in 2004. Solid bars denote the percent of all captures (n = 18).

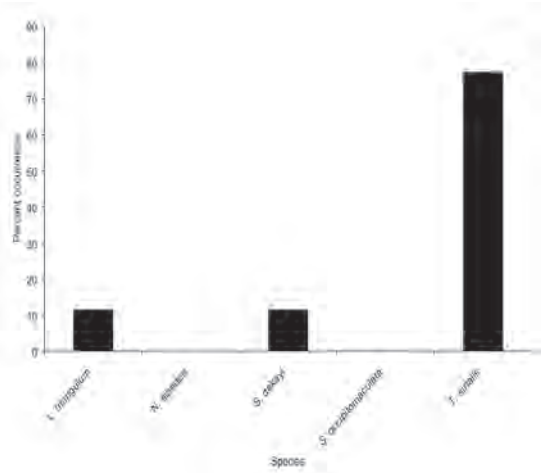

Figure 14. Relative abundance of snakes at the Mulch site at James H. Barrow Field Station, Portage County, Ohio, USA, during 2002-2004. Solid bars denote the percent of all captures (n = 44).

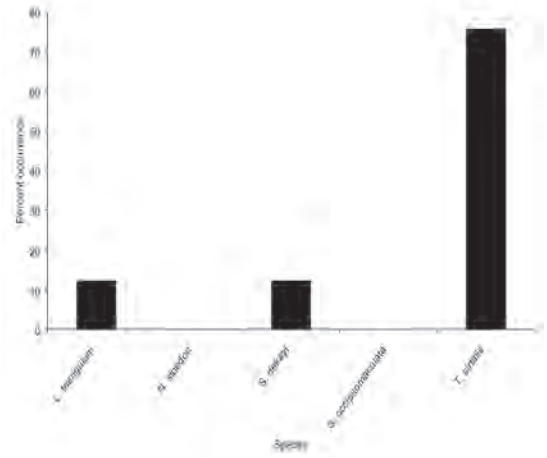

Figure 15. Relative abundance of snakes at the Oil Well site at James H. Barrow Field Station, Portage County, Ohio, USA, during 2001-2004. Solid bars denote the percent of all captures (n = 90).

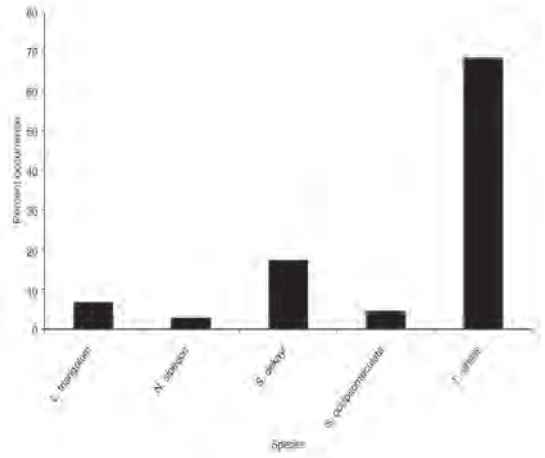

Figure 16. Relative abundance of snakes at the Old Field site at James H. Barrow Field Station, Portage County, Ohio, USA, during 2001-2004. Solid bars denote the percent of all captures (n = 281).

either measure of abundance, the Midland Rat Snake and Eastern Racer (*Coluber constrictor*) were the two dominant species and were followed distantly in numbers of captures of other species (Fig. 11). Numbers of snakes/cover board were relatively low for all captures (5.8 snakes/ cover board) and all new captures (4.4 snakes/ cover board). Mean body sizes of nine Eastern Racers (mean = 107.2 + 13.5 cm SVL; range = 83-123) and 11 Midland Rat Snakes (mean = 108.4 + 13.5 cm SVL; range = 96.5-135). Body sizes of two Eastern Hognose Snakes (*Heterodon platirhinos*) were also large in body size (77, 64 cm SVL). Seven Timber Rattlesnake (*Crotalus horridus*) sightings in the study areas in 2005 were of adults > 1.5 m TL.

A Five-lined Skink (*Plestiodon fasciatus*) was captured under cover boards on 8 June and on 2 August in parts of the grassland. The following additional species were seen at FITG

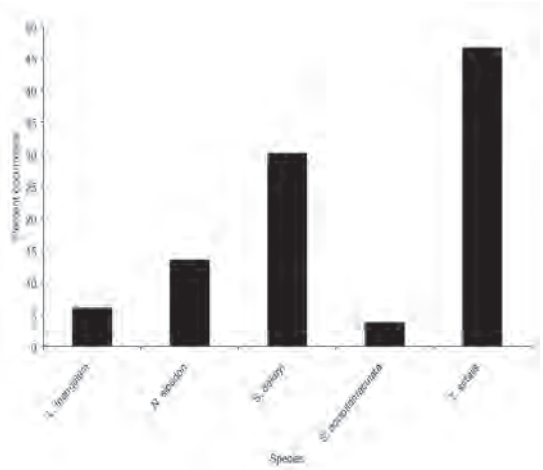

Figure 17. Relative abundance of snakes at the Wet site at James H. Barrow Field Station, Portage County, Ohio, USA, during 2001-2004. Solid bars denote the percent of all captures (n = 133).

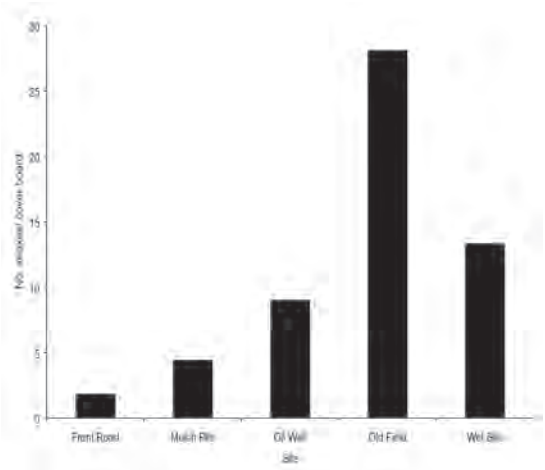

Figure 18. Number of snakes/cover board at all five grassland sites combined at James H. Barrow Field Station, Portage County, Ohio, USA, 2001-2004. Solid bars denote percent of all captures (n = 566).

during the study: Common Snapping Turtle (*Chelydra serpentina*), Painted Turtle, and Box Turtle.

Wildwood Park

We recorded 92 total captures of 71 marked Common Garter Snakes at WP during 2001-2004. Numbers of snakes/cover board were intermediate for all captures (15.3 captures) and all new captures (8.8 captures). A single Spotted Salamander (*Ambystoma maculatum*) was found beneath one of the cover boards on 9 September 2005. A trail that passes through this site is used as nest sites by the Painted Turtle and Box Turtle. The following species were seen at WP during the study: American Toad (*Anaxyrus americanus*), Fowler's Toad (*A. fowleri*), Spring Peeper (*Pseudacris crucifer*), Bullfrog (*Lithobates catesbeianus*), Bronze Frog (*L. clamitans*), Pickerel Frog (*L. palustris*), Northern Dusky Salamander (*Desmognathus fuscus*), Northern Two-lined Salamander (*Eurycea bislineata*), Northern Redback Salamander (*Plethodon cinereus*), Common Snapping turtle, and Brown Snake (*Storeria dekayi*). WEM was told of reports of the Wood Turtle (*Glyptemys insculpta*) and a single sighting of the Midland Rat Snake (*Scotophis spiloides*).

James H. Barrow Field Station

We recorded 565 total captures of five species that were caught during 2001-2004. For all sites combined, the Common Garter Snake was the most abundant species accounting for 65.2% of all snake captures during the study (Fig. 12). The Brown Snake was second in abundance for all sites combined when measured by all captures (18.9%) (Fig. 12). Overwhelming dominance of the Common Garter Snake on the station's grasslands was evident at each of the five sites (Figs. 13-17). However, the distribution and composition varied greatly among the remaining species. Likewise, the overall abundance of snakes, as measured by total numbers of snakes/cover board, varied extensively among sites (Fig. 18). Three snake species co-occurred at two sites (Figs. 14, 15), four species co-occurred at one site (Fig. 13), and five species co-occurred at two sites (Figs. 16, 17). Snakes co-occurring with the Common Garter Snake were generally low in abundance. Exceptionally, the Brown Snake, which co-occurred at all five sites, was clearly the second most frequently encountered species at Old Field (Fig. 16) and the Wet Depression site (Fig. 17). At remaining sites, the Brown Snake occurred at abundances equal to or exceeding those of synoptic species (Figs. 13-15). With respect to number of snakes captured/cover board, Front Road was the least productive

Figure 19. *Thamnophis sirtalis* at PNR. Photograph by Robert S. Mulvihill. ◄

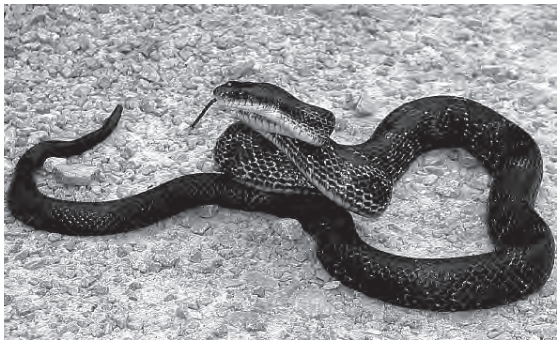

Figure 20. *Scotophis spiloides* at PNR. Photograph by Robert S. Mulvihill. ▲

Figure 21. *Coluber constrictor* at FITG. Photograph by Dave Zapotok. ◄

(1.8 snakes/cover board), and Old Field was the most productive (28.1 snakes/cover board) (Fig. 18). No other reptiles or amphibians were found under the cover boards; however, the following species were seen on the station during the study: Northern Dusky Salamander, Eastern Newt (*Notophthalmus viridescens*), Redback Salamander, Spring Peeper, Bullfrog, Bronze Frog, Pickerel Frog and Midland Rat Snake.

DISCUSSION

Common to 13 of the 15 sites, in three of the four main study areas, the Common Garter Snake (Fig. 19) was consistently the most frequently encountered snake. The second most frequently observed species was nearly always a small fossorial species, such as the Brown Snake, Redbelly Snake, or Ringneck Snake. In sharp contrast, large individuals of the Midland Rat Snake (Fig. 20) and the Eastern Racer (Fig. 21) were most abundant in a large grassland. At that same study area, other species were large in body size, only one Ringneck Snake was captured and the Common Garter Snake was not encountered.

Isolation and small size of the grassland patches were associated with the absence of the Eastern Racer, a large-bodied and wide-ranging species, in our study and another study (< 10 ha) (Kjoss & Litvaitis, 2001) in the northeastern United States. In this regard, the Eastern Racer, once common in the more open habitat of PNR, was subsequently found to have been rare in connection with forest encroachment (Meshaka et al., 2008a). Its absence from smaller grasslands could have been a response to the need for increased home range size by this large snake.

Kjoss & Litvaitis (2001) found that fewer small species of snakes, and larger individuals of those species, were found in areas intensively used by the Eastern Racer. They attributed those results to predation by the Eastern Racer. Similarly, we found large individuals only of large-bodied (e.g., Eastern Racer and Midland Rat Snake) and stout-bodied (Eastern Hognose Snake and Timber Rattlesnake) species, and only one individual of a small-bodied snake (Northern Ringneck Snake) at the 101-ha site at FITG. We suggest that predation by the Eastern Racer, whose diet includes a wide range of snakes (Palmer & Braswell, 1985; Klemens, 1993; Hulse et al., 2001) was responsible for these findings. In the absence of the Eastern Racer, small species and juveniles were encountered among the snakes found

at PNR (Meshaka, 2009a) and JHBFS (Meshaka et al., 2008b), and juvenile Common Garter snakes were encountered at WP (Meshaka, 2009b).

Like Kjoss & Litvaitis (2001) who found only the Common Garter Snake in the smallest patches (< 1.5 ha), we found only the Common Garter Snake in one of our smallest patches. Kjoss & Litvaitis (2001) attributed the absence of other species in the smallest patches to insufficient soil moisture because of frequent mowing. In support of this explanation in our study, at two of the four main study sites in which the Brown Snake had been recorded, it was the annually mown site at WP that did not have this species in the grassland. On the other hand, JHBFS also had very small patches of grassland but were in various stages of oldfield succession. For example, Oil Well was even smaller (0.2 ha) than the site at WP, but was inhabited by three snake species. Thus, the Common Garter Snake patches were small, but not restricted to the Common Garter Snake.

Dominance of the Common Garter Snake with varying combinations and frequencies of other small-bodied species was found in larger patches studied by Kjoss & Litvaitis (2001). Regarding Common Garter Snake dominance, in our study this finding was generally but not exclusively the case. For instance, at one of eight sites at PNR total captures of the Common Garter Snake exceeded those of the Redbelly Snake and the opposite was true concerning new captures. One testable explanation of this departure is the short duration, 2008-2009, of study at this site. On the other hand, as yet unknown features of the habitat may have inhibited the success of the Common Garter Snake at this site. Among the syntopic snakes in Common Garter Snake dominated sites, second place in captures by small-bodied earthworm or slug-eating species was the general pattern. That they did not occur in greater abundance than they did, we attribute to competition for a shared food resource with, and to some extent predation by, the Common Garter Snake as testable explanations. In this connection, the Common Garter Snake was reported to have fed primarily on earthworms in Pennsylvania (Hulse et al., 2001) and on earthworms and amphibians in Indiana (Minton, 2001) and New York (Hamilton, 1951). In the latter study, snakes were also eaten in low frequencies. Habitat quality is also a testable explanation. Highest numbers of PNR Ringneck Snakes were found along the two pasture edges of an infrequently mowed site and less so along the edges of an annually mowed site. To this end, the Ringneck Snake was sensitive to the successional changes in grassland whereby population sizes increased shortly after the removal of cattle and growth of dense ground cover or tall grass, and began to diminish at varying points in which open habitat was lost to canopy and eventual forest (Fitch, 1991). In this same study, the Brown Snake and the Common Garter Snake were least affected by the successional changes, such that their initial population increases were followed by relatively stable population sizes. In the case of the Common Garter Snake, temporal variation in its abundance was found to have been affected more by annual changes in weather than by the succession (Fitch, 1999).

In remaining cases, larger-bodied vertebrate-eating snakes, such as the Midland Rat Snake and Milk Snake, occurred at similar or greater abundances than their earthworm and slug-eating counterparts in Common Garter Snake dominated sites. Variation in their abundance may have been related not only to the size of the patch, but, also adjoining habitat, succession of the site, its isolation from other patches, and sample size. For instance, nearby ponds, thicket and buildings, including a shed which contained two recaptured individuals from Crisp Meadow, enhanced the habitat for the Midland Rat Snake. Also at this site and Friedline Original, cover boards were set along the edge that might have been analogous to the presence of tree and shrub cover that was interspersed in the openness at FITG where this species was also captured.

Ophiophagous as a juvenile and primarily a mammal-eater as an adult in Pennsylvania (Hulse et al., 2001), the Milk Snake would have existed as a predator of the Common Garter Snake for part of its life and apart from potential competition for prey with that species throughout its life where it maintained some presence in larger fields at PNR. The heavily canopied deciduous forest surrounding the smaller patches would have enforced the rarity of this species in small patches. Not surprisingly,

this species was unknown in the heavily wooded WP. On the other hand, the small grassland sites at JHBFS were separated by thicket that would not have hindered its movements among oldfield patches of our study and would themselves have served as habitat for this species. In this regard, after initial increases in population sizes following cattle removal, the Eastern Racer, the Milk Snake and the Northern Water Snake were negatively impacted by forest encroachment. The Midland Rat Snake and the Brown Snake were least affected by the successional changes, such that their initial population increases were followed by relatively stable population sizes (Fitch, 1999). Sample size also could have played a role in the observed frequencies of the Milk Snake. For example, it was expected but not captured during a single season of trapping in the expansive grassland of FITG. Likewise sample size was too small for us to determine if the similarity of total numbers of the Milk Snake and the Redbelly Snake at Friedline Foundation was the norm for this site. Snake diversity was a correlate of large patch size in the study by Kjoss & Litvaitis (2001). At a macro-level, large overall area of three study areas was associated with high numbers of snake species. Connections among patches and proximity to human disturbance were present in all but WP whose grassland snake assemblage was comprised of only the Common Garter Snake. Possibly, the connections were sufficient to support a rich snake assemblage but not large enough to include the Eastern Racer.

Our findings corroborate the role of patch size in grassland snake assemblage structure. Large patches could support more species including the Eastern Racer, an ophiophage in part, whose presence affected the composition, evenness and population structure of the assemblage. In its absence, the Common Garter Snake, a prey species of the Eastern Racer, was found to have been a dominant component of otherwise highly uneven assemblages. Whereas competition for food and perhaps predation are potential explanations for the variation in abundances of some of the species, for other species structural composition of the habitat appeared to have played a role (e.g., Ringneck Snake, Brown Snake) or primary role (Midland Rat Snake, Milk Snake) in determining abundances in these latter sites. Consequently, whereas large parcels of early successional and shrub-dominated habitats are necessary for the conservation of the Eastern Racer in the northeastern United States (Kjoss & Litvaitis, 2001), attention should also be paid to responses of ecological succession in grasslands regardless of size by individuals snakes species in this region of North America.

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