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SEASONAL ACTIVITY AND BREEDING SEASONS OF SNAKES FROM POWDERMILL NATURE RESERVE IN WESTERN PENNSYLVANIA: THE IMPORTANCE OF SITE-SPECIFIC DATA IN LAND MANAGEMENT PROGRAMS

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ABSTRACT.—Grasslands are rare yet biologically rich habitats in the northeastern United States, including Pennsylvania. I examined the seasonal activity and aspects of reproduction of a grassland snake assemblage during 2002-2009 at Powdermill Nature Reserve in western Pennsylvania. Peak activity for the eight species captured under cover boards occurred in June. Most gravid females of this assemblage collectively were evident during May-July, spent females appeared as early as June, and no gravid females occurred after August. The activity patterns of this assemblage conformed to the stronger seasonal constraints typically associated with northerly populations. However, differences were evident among and within species when compared to other northerly populations. The temporally localized peak in activity of the ophidian segment of this grassland community must be considered when timing land management programs such as prescribed burning, disking, or mowing that are necessary to maintain the integrity of this vanishing habitat.

Key Words.—conservation; ecology; grasslands; management; Pennsylvania; Powdermill Nature Reserve; snakes

INTRODUCTION

Grasslands, a historically important component of the United States, have declined by 80% range-wide since the mid-1800s (Brennan and Kuvlesky 2005). In the northeast, most grassland loss arises from its succession to the climax forest (Brennan and Kuvlesky 2005). This habitat has come under scrutiny with respect to management in light of its fragmentation and associated sensitive species.

Grasslands occurred widely in Pennsylvania since the most recent glacial retreat 11,000 years ago. Historically, large grazing animals and fires set by Native Americans maintained grassland habitats in Pennsylvania. Subsequently, European settlers sustained this habitat through land clearing. The latter group reduced forests to approximately 25% of their former coverage and, in a reversal of coverage, approximately 25% of Pennsylvania's habitats are open today (Duncan, P.S. 2005. Pennsylvania Comprehensive Wildlife Conservation Strategy. Unpublished Pennsylvania Game Commission and Pennsylvania Fish and Boat Commission Report. 762 p.).

The importance of this currently rare habitat in Pennsylvania is reflected in the negative impacts to a wide range of species associated with the loss and fragmentation of this habitat. For example, the Regal Fritillary Butterfly (*Speyeria idalia*), once widespread in the state, is currently restricted to a single grassland site in south-central Pennsylvania (Ferster 2005; Ferster et al. 2008). Duncan (2005) lists 37 vertebrate species known to inhabit Pennsylvania grasslands. Among those species known by Duncan (2005) to be negatively impacted with respect to population sizes and geographic distributions by the loss and fragmentation of this habitat were the Grasshopper Sparrow (*Ammodramus savannarum*), Vesper Sparrow (*Pooecetes graminus*), Loggerhead Shrike (*Lanius ludovicianus*), and Northern Bobwhite (*Colinus virginianus*), and mammals such as the Least Shrew (*Cryptotis parva*) and Spotted Skunk (*Spilogale putorius*).

Grassland patch size and shape can affect grassland birds (e.g., Bajema and Lima 2001; Balent and Norment 2003; Davis 2004). Likewise, grassland management techniques such as burning, mowing, haying, and disking, vary in their effects on the biotic community depending on the timing of their implementation (Fynn et al. 2004), frequency of use (Swengel 2001a), size of the area subjected to the activities (Swengel 2001b), and the simultaneous implementation of other procedures (Swengel 1998). Among management techniques, burning has been reported as a source of mortality for some amphibians and reptiles, although quantification of fire-induced mortality is not as well known (Russell et al. 1999). In Pennsylvania, mowing is the primary management tactic for grasslands..

However, at Fort Indiantown Gap Training Center in south-central Pennsylvania, tanks incidentally maintain the state's largest contiguous grassland. These "iron bison" notably mimic the natural underfoot disturbance and clearing by large Pleistocene herbivores (Ferster 2005; Ferster et al. 2008). Thus, the dynamics of

grasslands in the Northeast are of interest with great opportunity for private landowner involvement and benefit in their conservation.

Four amphibians and nine reptiles are in Pennsylvania's Wildlife Action Plan's priority species list for Pennsylvania grassland habitats (see Duncan 2005 *op. cit.*), and the state lists one reptile, the Short-headed Garter Snake (*Thamnophis brachystoma*), as rare. Nevertheless, neither the role of this snake in the grassland ecosystem, nor the effects of management techniques on amphibian and reptiles are well known for this state.

I examined the seasonal activity patterns and reproductive characteristics of a western Allegheny grassland snake assemblage comprised of eight species (Meshaka et al. 2009) from a 29.4 ha grassland matrix on a 856.2 ha protected nature reserve in western Pennsylvania. I asked two questions; how do the patterns in seasonal activity, a geographically variable life history trait, of the snake assemblage compare with other populations, and how can these findings be applied to the effective management of northeastern grasslands?

MATERIALS AND METHODS

Study site.—The Carnegie Museum of Natural History owns and operates the Powdermill Nature Reserve (PNR) where I conducted this study. The PNR is an 856.2 ha reserve that is in Rector, Westmoreland County, Pennsylvania, USA. The previously farmed tracts became reforested since its founding in 1957 so that today, 89.5% of PNR habitat is mixed forest. Primary and secondary grassland (< 5.0%) is now a considerably smaller component of its terrestrial habitat.

Methods.—I visited up to eight grassland sites once each month during September 2002, June-September 2003, May-October 2004, and May-September of 2005-2009. I placed 1 × 3 m corrugated metal cover "boards" at each of the grassland sites. The number of sites increased over the years, and the number of cover boards decreased in two sites (Meshaka et al. 2009). Early (May-June) and late (September-October) in the season, I checked the cover boards in late morning to early afternoon. During July-August, I checked the cover boards early in the morning before snakes became active and left their retreats or very late in the afternoon when snakes had returned for the night. On some of these occasions, a second day was necessary to visit all sites before snakes left increasingly hot cover boards.

Immediately upon capture, I sexed and measured the snout-vent length (SVL) of snakes. I next fitted snakes with an AVID Passive Integrated Transponder (PIT) tag for individual identification unless they were smaller than 15 cm SVL, in which case I marked them as an annual cohort by clipping a belly scale. After processing, I released the snakes at the cover board of capture.

I restricted use of seasonal activity data to those snakes that I captured under cover boards during the study period of May-September during 2003-2009. I based monthly activity values on the number of all captures of a particular species. I derived data for body size from all initial snake captures during 2002-2009 from under cover boards as well as opportunistic captures.

I based minimum body size at sexual maturity for females on the smallest gravid female that I observed among large samples. Otherwise, sexual body size minima were taken from Hulse et al. (2001). Exceptionally, sexually mature males of the Common Garter Snake were apparent at body sizes slightly smaller than those reported by Hulse et al. (2001). Means are followed by ± 2 standard deviations. Statistical significance was recognized at $P < 0.05$.

RESULTS

The snake species associated with grassland habitats were a subset of the 13 snake species previously reported from the station (Meshaka et al. 2008a) and the 22 snake species known from Pennsylvania (Meshaka and Collins 2009). The first representative of each species in my study appeared in June 2003 (*Diadophis punctatus, Liochlorohis vernalis, Storeria coccipitomaculata, Thamnophis sirtalis*), August 2003 (*Nerodia sipedon*), June 2004 (*Scotophis spiloides*), August 2004 (*Lampropeltis triangulum*), and June 2007 (*Crotalus horridus*).

Crotalus horridus.—The Timber Rattlesnake was seen on two occasions on the same cover board at Crisp Meadow in June and July 2007. Based on its appearance, it was presumed to have been the same adult.

Diadophis punctatus. —The Ringneck Snake (88 observations) was present during May-September and was most often encountered in June (Fig. 1a). Its peak activity month mirrored that of the station's snake assemblage (Fig. 2). Male and female activity extended during May-September and peaked in June. A smaller second peak in male activity occurred in September (Fig. 3a). Male-female groups were found in May (n = 1), June (n = 3), August (n = 1), and September (n = 1). Juveniles appeared during May-September, but their activity also peaked in June (Fig. 3a). Gravid females were captured during May-June, spent females were captured during June-July (Fig. 4a), and the smallest spent female measured 23.5 cm SVL. The Ringneck Snake may have been the earliest species to give birth at PNR. Its egglaying season ended during the peak gravid months of the other snakes at PNR (Figs. 4a and 4b).

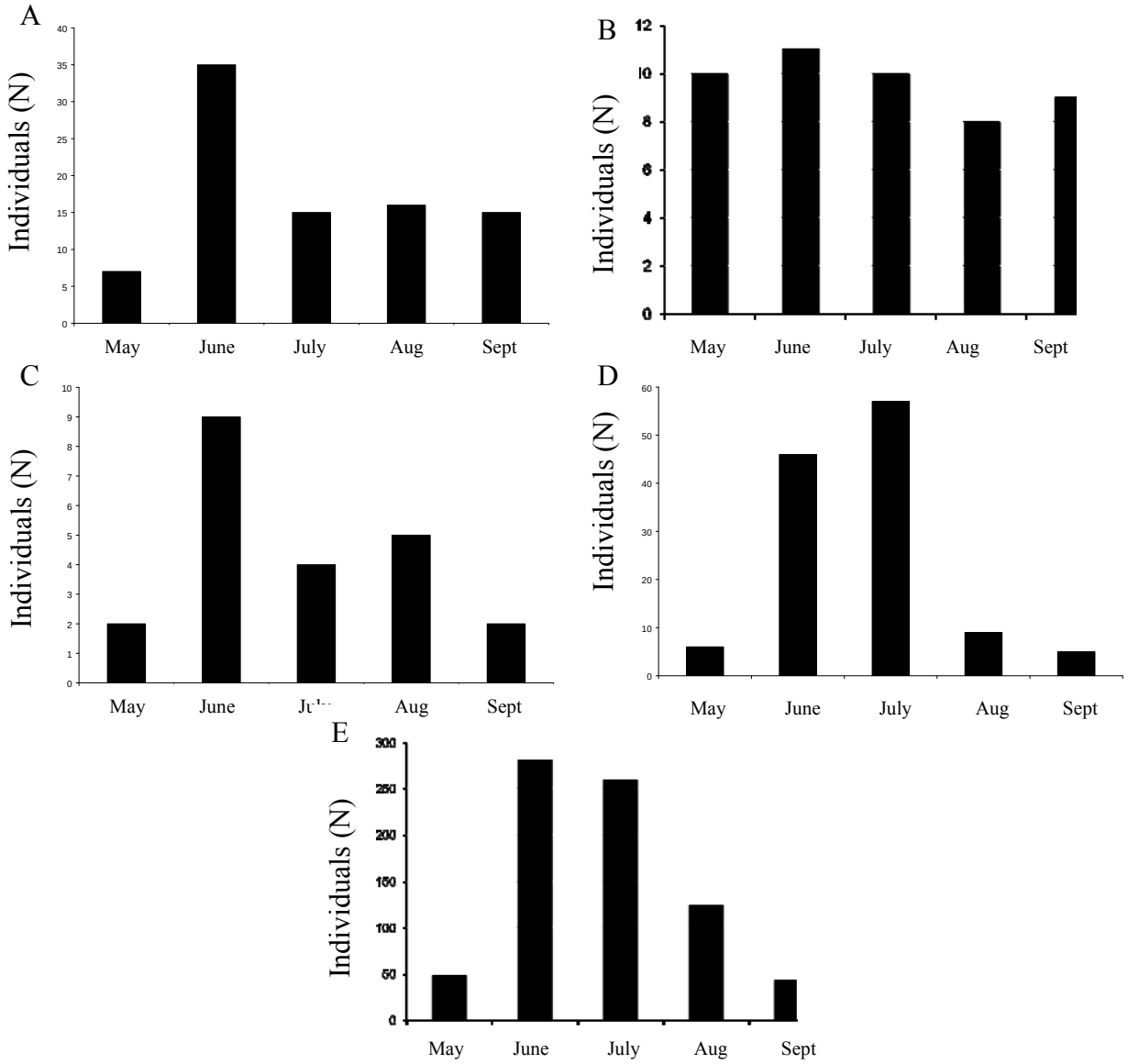

FIGURE 1. Seasonal activity of the: (A) Ringneck Snake (*Diadophis punctatus*) (n = 88) (These data include three snakes of unknown sex or size-class); (B) Milk Snake (*Lampropeltis triangulum*) (n = 48); (C) Midland Rat Snake (*Scotophis spiloides*) (n = 22); (D) Redbelly Snake (*Storeriea occipitomaculata*) (n = 123) (These data include one snake of unknown sex or size-class); (E) Common Garter Snake (*Thamnophis sirtalis*) (n = 718) (These data include 37 snakes of unknown sex or size-class) during 2003-2009 at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA.

The smallest Ringneck Snakes (11.4 cm SVL) appeared in May and June (Fig. 5a) and the seasonal distribution of body sizes suggests that sexual maturity occurred at ~ one year of age (Fig. 5a). Body size of males (mean = 27.9 ± 4.85 cm SVL; range = 18.4–38.7; n = 26) was significantly different from that of females (mean = 27.7 ± 3.45 cm SVL; range = 21.0–35.6; n = 30) with respect to the variance ($F = 0.5046$, $P < 0.04$) but not the mean ($P > 0.05$). The male: female sex ratio of 60 new captures was 0.89:1.

Lampropeltis triangulum.—The Milk Snake (48 observations) was active during May-September, with most captures having occurred somewhat more often in June and July (Fig. 1b). In contrast, other snakes were distinctly more commonly encountered during June-July (Fig. 2). I observed males in relatively even numbers during May-September, whereas I found the fewest females in August during this time (Fig. 3b). I captured a few juveniles throughout the season with slightly more in August than in other months (Fig. 3b). Males and females occurred together under cover boards in May (n = 3) and once in each of June, July, and August. Two females (69.9 & 86.4 cm SVL) were gravid in June, and spent females were present in July (n = 2) and September (n = 1), the smallest of which measured 64.8

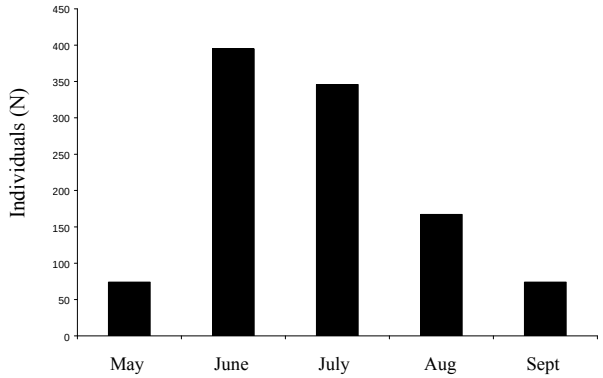

FIGURE 2. Seasonal activity of the eight species of snakes (n = 1056) during 2003-2009 at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA. These data include 41 snakes of unknown sex or size-class.

cm SVL. Numbers of gravid snakes at PNR generally peaked in June and July (Fig. 4b). Six males (mean SVL = 68.0 ± 12.1 cm; range = 54.6–81.3) and six females (mean SVL = 66.0 ± 12.0 cm SVL; range = 54.0–86.4) used the cover boards during my study. The male: female sex ratio of 12 new captures was 1.00:1.

***Liochlorophis vernalis*.—**The Smooth Green Snake (13 observations) was under cover boards in June and August with males encountered in both months, and nearly all females restricted to June (Fig. 3c). The activity season of this species was shorter than that of the rest of the snake assemblage but also peaked in activity in June (Fig. 2). I found a single male-female pair under the cover boards in each of June and August.

The smallest SVL of a gravid female was 28.6 cm. All nine females captured in June were gravid. I captured three males (SVL = 26.7, 29.2, 30.5 cm) and seven females (mean SVL = 34.4 ± 6.58 cm; range = 25.7–44.5). The male: female sex ratio of 11 new captures was 0.38:1.

***Nerodia sipedon.*—**The Northern Water Snake (5 observations) occurred under cover boards during May-August; May (n = 1), June (n = 1), and August (n = 3). Females were captured in May and August, and juveniles were captured in June and August under cover boards. From individuals at the station, I have measurements for two males (47.6 & 54.6 cm SVL) and eight females (mean SVL = 71.7 $\pm$ 12.9 cm; range = 52.7-84.5).

***Scotophis spiloides.*—**The Midland Rat Snake (22 observations) occurred during May-September with peak occurrences in June (Fig. 1c). Duration of the active season and peak activity month of the Midland Rat Snake were similar to those of the snake assemblage (Fig. 2). Males were active during June-August, with an apparent bimodality with their seasonal use of the cover boards, and females were found sporadically during May-September (Fig. 3d). The smaller of two juveniles captured in June, a female, measured 58.4 cm SVL. I observed no gravid or spent female Midland Rat Snakes, and no male-female pairs or groups under the cover boards. I captured 11 males (mean SVL = 114.0 ± 19.3 cm; range = 78.7–147.3) and four females (mean SVL = 112.6 $\pm$ 10.7 cm; range = 99.7-123.2) during this study. The male: female sex ratio of 13 new captures was 2.25:1.

***Storeria occipitomaculata.*—**The Redbelly Snake (123 observations) was active during May-September, with peak activity in July (Fig. 1d). Both of these patterns mirrored those of the overall snake assemblage (Fig. 2). A few males occurred in June, August, and September (Fig. 3e). Females occurred more frequently and appeared throughout the season with most observations in July, followed by an abrupt decline thereafter. Juveniles were present in June and July (Fig. 3e). Male-female groups appeared under cover boards in June (n = 3) and September (n = 2). To that end, a male (22.2 cm SVL) and female (24.1 cm SVL) were found in copula under a cover board on 11 September 2009. The smallest gravid female measured was SVL = 21.0 cm. All females captured in May, and nearly all females captured in June and July were gravid (Fig. 4c). The birthing season ended one month earlier than the egg laying/birthing season of the snake assemblage in general (Fig. 4b). However, the May-July pulse in the frequency of gravid females was similar to that of the assemblage (Fig. 4b). Spent females occurred in August (Fig. 4c), whereas spent females for all snakes at PNR occurred during June-September, with a late-summer peak in frequency (Fig. 4b). Rate of growth among Redbelly Snakes was unclear from the seasonal distribution of body sizes in this study (Fig. 5b). However, the smallest individual (14.6 cm) appeared in June, the smallest male (18.4 cm SVL) in September, and the smallest female (19.7 cm SVL) in June (Fig. 5b). Hatchlings in September could conceivably have reached sexual maturity at approximately their first birthday and mated that following fall. Mean body size of 11 males (21.8 $\pm$ 2.15 cm; range = 18.4-24.8) was significantly different (T = -4.388; df = 110; $P < 0.000$) than that of 101 females (25.0 ± 2.30 cm; range = 19.7–31.8). The male to female sex ratio of 110 new captures was 0.10:1.

***Thamnophis sirtalis.*—**The Common Garter Snake (755 observations) was active during May-September, with most activity in June and July (Fig. 1e). The same was true of the snake assemblage in general (Fig. 2) for

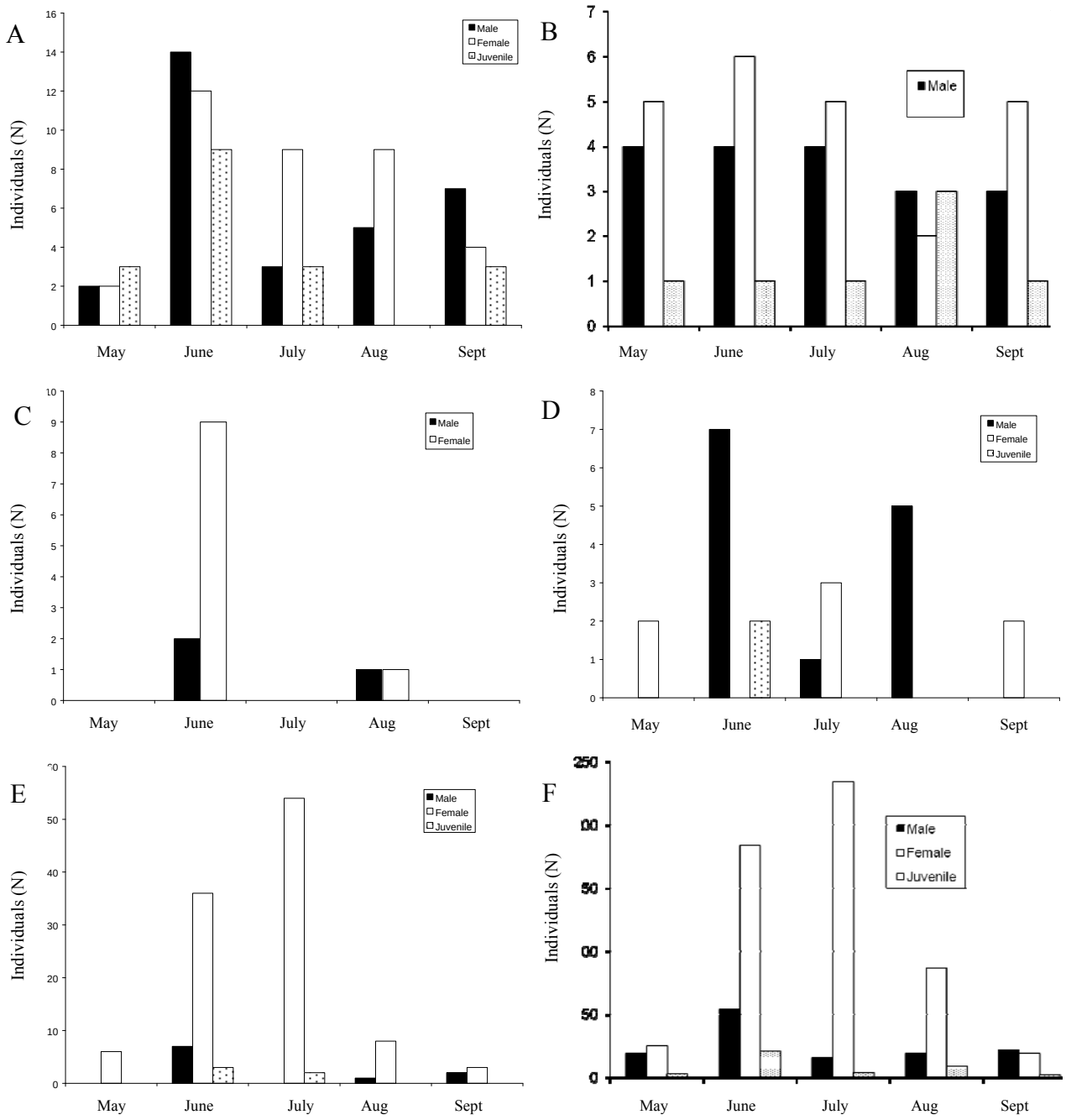

FIGURE 3. Seasonal activity of: (A) male (n = 31), female (n = 36), and juvenile (n = 18) Ringneck Snakes (*Diadophis punctatus*); (B) male (n = 18), female (n = 23), and juvenile (n = 7) Milk Snakes (*Lampropeltis triangulum*); (C) male (n = 3) and female (n = 10) Smooth Green Snakes (*Liochlorophis vernalis*); (D) male (n = 13), female (n = 7), and juvenile (n = 2) Midland Rat Snakes (*Scotophis spiloides*); (E) male (n = 10), female (n = 107), and juvenile (n = 5) Redbelly Snakes (*Storeria occipitomaculata*); (F) male (n = 130), female (n = 549), and juvenile (n = 39) Common Garter Snakes (*Thamnophis sirtalis*) during 2003-2009 at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA.

which this species comprised 71.6% of the total number of captures. Males were active during May-September, most noticeably in June (Fig. 3f). Females were active during the same months as males; however, their activity peaked in July, and quickly decreased over the rest of the season (Fig. 3f). A female (SVL = 45.1 cm) captured for the first time on 8 August 2004 in Crisp Meadow had a fresh laceration on her neck, probably from a rotary mower that was tested the day before in that field. Juveniles were present at low frequencies throughout May-September (Fig. 3f). Male-female groups under cover boards were present May-September, with the highest incidences occurring in June followed by a lesser peak during August-September (Fig. 6). The smallest

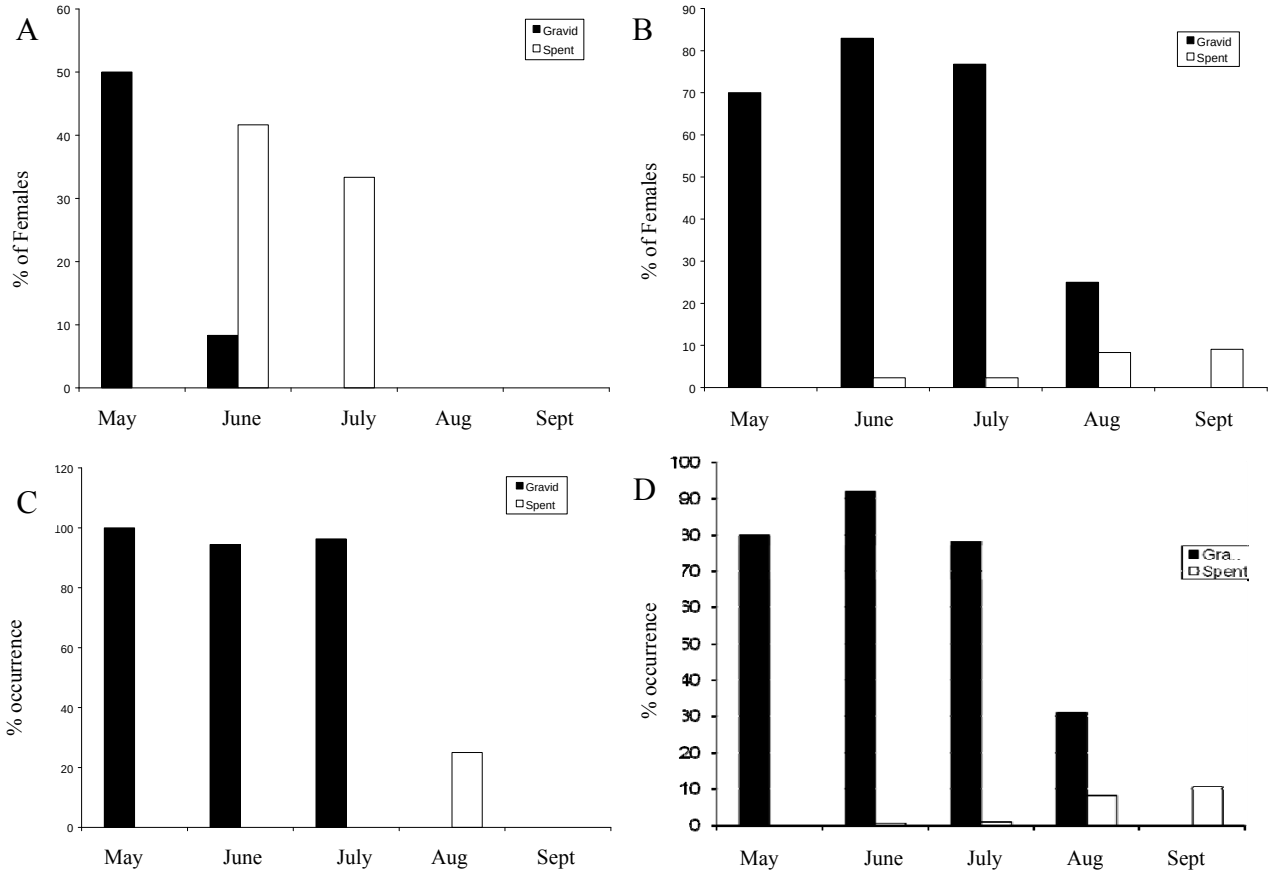

FIGURE 4. Seasonal frequency of gravid and spent females of (A) the Ringneck Snake (*Diadophis punctatus*) (n = 10); (B) five species of snakes (n = 529); (C) the Redbelly Snake (*Storeria occipitomaculata*) (n = 95); (D) the Common Garter Snake (*Thamnophis sirtalis*) (n = 399) during 2003-2009 at powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA.

gravid female measured 38.1 cm SVL. Females were gravid during May-August, with the highest incidences during May-July (Fig. 4d). Spent females were present during June-September, with most occurring during the latter two months of the season (Fig. 4d). The seasonal patterns of gravid and spent Common Garter Snakes mirrored those of the snake assemblage (Fig. 4b), which was not surprising in light of the overwhelming dominance of Common Garter Snake captures at PNR. The smallest individual (SVL = 13.4 cm) appeared in August (Figs. 7) and the smallest male was SVL = 26.0 cm (Fig. 7a). The seasonal distribution of body sizes suggested that sexual maturity in males could have occurred by the end of their first season or early in the following summer (Fig. 7a). Females born in August should have been sexually mature by the following August or September, and those born in June should have been sexually mature by the following June or July (Fig. 7b). Mean body size of 109 males (mean SVL = 39.6 ± 5.85 cm; range = 26.0–53.3) was significantly different (T = -13.526; df = 405; $P < 0.001$) than that of 298 females (mean SVL = 47.3 ± 6.41 cm; range = 38.1–67.8). The male: female sex ratio of 390 new captures was 0.27:1.

DISCUSSION

The primarily unimodal seasonal amplitudes in snake activity at PNR generally conformed to the seasonal activity patterns associated with north-temperate snakes (Gibbons and Semlitsch 1987). Furthermore, the seasonal constraint on activity was typical of northern populations (Klemens 1993), the seasonal duration of which was much less than that of southerly populations (e.g., Gibbons and Semlitsch 1987; Dalrymple et al. 1991). The seasonal activity patterns detected at PNR, however, varied among species during an otherwise limited annual time frame as well as geographically within these species. The same differences applied to reproductive timing. Consequently, these types of phenological data are necessary for formulating effective management strategies that are necessary for maintaining healthy grassland ecosystems.

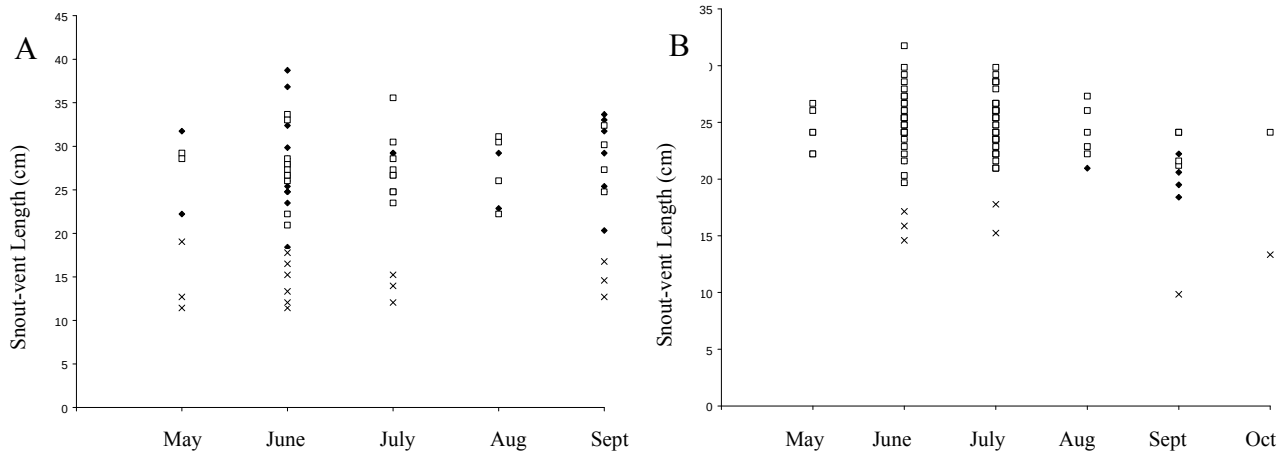

FIGURE 5. Seasonal distribution of body sizes of (A) male (n = 26), female (n = 30), and juvenile (n = 17) Ringneck Snakes (*Diadophis punctatus*) and (B) male (n = 11), female (n = 101), and juvenile (n = 7) Redbelly Snake (*Storeria occipitomaculata*) during 2002-2009 at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA. Symbols: × = juvenile, □ = female, ♦ = male.

Seasonal activity.—The Ringneck Snake exhibited a unimodal activity pattern, which peaked in June, at PNR (this study) and in Pennsylvania generally (Meshaka and Wilkerson 2008). Ringneck Snakes from South Carolina (Gibbons and Semlitsch 1987) and the southern Everglades (Dalrymple et al. 1991) also exhibited unimodal seasonal activity. However, differences in the timing of peak activity existed among species. For example, although June was the most active month for Ringneck Snakes in Pennsylvania and in South Carolina (Gibbons and Semlitsch 1987), peak activity occurred in June-July in the southern Everglades (Dalrymple et al. 1991). In the Everglades, a June peak in male activity and a July peak in female activity were present, whereas males may have had June and September peaks in their activity PNR.

Milk Snakes at PNR exhibited unimodal activity that peaked in June, although previous reports detected unimodal activity in Pennsylvania having peaked in May (Hulse et al. 2001). A difference in data collection methods and the statewide approach by Hulse et al. (2001) could have accounted for these differences. Like that of PNR, the seasonal activity pattern of Milk Snakes in northeastern Ohio was unimodal with a single peak in June (Meshaka et al. 2008b). I am unsure if the bimodality of female activity at PNR was actual or an artifact of a limited sample size.

At PNR, the Midland Rat Snake was unimodal in its seasonal activity, with a peak in June. Bimodal seasonal activity, with progressively longer intervals between seasonal activity peaks, was evident in Maryland (May-June and September; Stickel et al. 1980), Kansas (April-May and September; Fitch 1963), and extreme southern Florida (May and October; Dalrymple et al. 1991). To that end, males which outnumbered females in numbers of new and total captures at PNR, exhibited a distinctly bimodal pattern to their seasonal activity with June and August peaks. Males were also much more common than females in extreme southern Florida (Dalrymple et al. 1991) but not in Maryland (Stickel et al. 1980). Large home ranges and greater movement by males and perhaps the short-term nature of studies best explain the male bias in Pennsylvania and Florida. For this reason, I can only speculate that smaller home ranges movements or perhaps the longterm nature of the study account for the differences found in Maryland by Stickel et al. (1980).

Seasonal activity of the Redbelly Snake was unimodal at PNR, with peak activity in July. In Pennsylvania, activity generally remained constant during May-August, tapered off in September, and surface activity ended by mid-October (Hulse et al. 2001). Too few males were captured at PNR to determine the modality of their seasonal activity pattern. Tentatively, males appeared to have been active under the cover boards primarily in June and subsequently in lesser numbers at

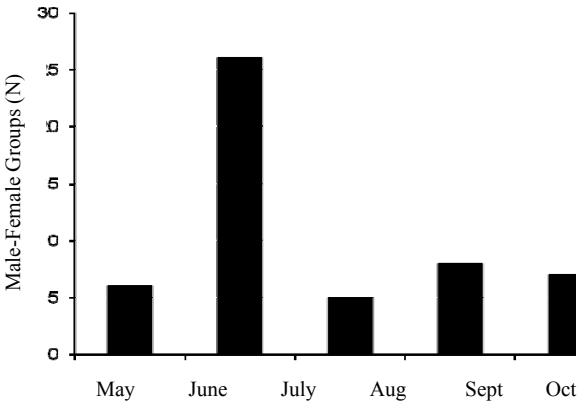

FIGURE 6. Seasonal distribution of mixed sex groups of the Common Garter Snake (*Thamnophis sirtalis*) (n = 52) during 2003-2009 at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA.

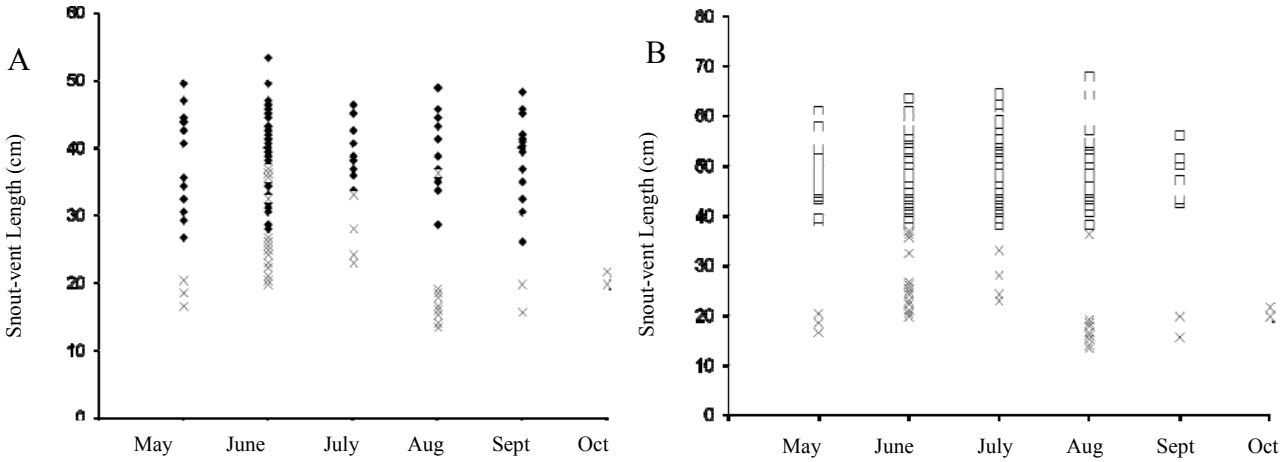

FIGURE 7. Seasonal distribution of body sizes of (A) males (n = 109) and juveniles (n = 41) and (B) of females (n = 298) and juveniles (n = 41) of the Common Garter Snake (*Thamnophis sirtalis*) during 2002-2009 at Powdermill Nature Reserve, Westmoreland County, Pennsylvania, USA. Symbols: × = juvenile, □ = female, ♦ = male.

the end of summer. Female Redbelly Snakes at PNR were distinctively unimodal in their seasonal activity pattern, with a July peak in association with their gravid condition. In northeastern Ohio, captures of this species were strongly bimodal (females in June, juveniles in September; Meshaka et al. 2008b). In South Carolina (Semlitsch 1987), seasonal activity of the Redbelly Snake was unimodal; however, the peak in activity occurred later (August-September; Gibbons and Semlitsch 1987). Interestingly, despite a large sample size of Redbelly Snakes, very few males appeared at PNR, and no males were found in northeastern Ohio (Meshaka et al. 2008b). The scarcity or absence of males in these two cover board studies could reflect a sampling bias if females differentially used surface cover almost exclusively when gravid.

The Common Garter Snake was by far the most abundant snake at PNR. Seasonal activity was unimodal at PNR like at a residential site in south-central Pennsylvania (Meshaka 2009) and for Pennsylvania in general (Hulse et al. 2001). However, activity was bimodal for an urban park site in south-central Pennsylvania (Meshaka 2009). Peaks in captures varied from May to September among these Pennsylvania studies. A unimodal seasonal activity pattern was present for this species in Michigan with an activity peak during April-May (Carpenter 1952). However, bimodal pulses occurred in northeastern Ohio (May and August; Meshaka et al. 2008b) and in the southern Everglades (July and October; Dalrymple et al. 1991). The time between seasonal amplitudes in activity was greater in the latter population. Females were far more common than males at PNR (Meshaka et al. 2009; this study), in northeastern Ohio (Meshaka et al. 2009), and in the southern Everglades (Dalrymple et al. 1991). Thus, number and timing of seasonal activity peaks and sex ratios varied interspecifically at PNR and intraspecifically across respective geographic ranges.

Mating seasons.—Variation in the timing of the mating season existed among these species. For example, with limited data mixed sex groups were observed during spring-summer (Milk Snake), summer (Smooth Green Snake) and early summer and fall (Redbelly Snake). For the Common Garter Snake generally, mating began in spring, and early summer appeared to be the primary but not the exclusive mating season (Rossman et al. 1996). Hulse et al. (2001) suggested the possibility of fall mating in Pennsylvania and this appeared to be the case at PNR. The seasonal distribution of mixed sex groups at the station suggested that mating probably occurred throughout the active season, primarily in June followed by a secondary breeding season during August-September. If the seasonal occurrence of mixed sex groups reflected mating behavior, the timing would be especially important for first time breeders recruiting into the population the following late summer of their lives in which case they would have an early opportunity to mate instead of having to wait until the following spring. Thus, seasonal peaks in the gravid and post-partum conditions were evident among PNR snake species and within these species across their respective geographic ranges.

Egg laying and birthing seasons.—The timing of egg laying and live birth at PNR also varied among species and within species compared to previous studies conducted elsewhere. Although PNR snakes were gravid during May-August, oviposition or parturition could occur earlier as in the Ringneck Snake (June and July), or later as in the Redbelly Snake (until August), and the Common Garter Snake (June-September,

especially August and September). In Pennsylvania, Ringneck Snakes oviposited from the end of June through very early July (Hulse et al. 2001), mid-June to August (Surface 1906), and May-August with very few gravid females found after June (Meshaka and Wilkerson 2008). Similarly, in Maryland (Clark et al. 1997) and New Jersey (Price 1975), oviposition took place from mid-June to mid-July. In North Carolina, most Ringneck Snakes were gravid in June but none thereafter (Palmer and Braswell 1995), and eggs were laid July in northeastern Kansas (Fitch 1999). In the southern Everglades, females were gravid during April-July, and captive snakes laid eggs during May-August (Dalrymple et al. 1991). These studies present breeding seasons of PNR snakes that were similar to other regions apart from extreme southern Florida.

Hatching of Ringneck Snakes during July-August at PNR led to a primary cohort that reached sexual maturity by mid- to late summer of the following year. This primary cohort would have had an adaptive advantage due to its early maturity, thereby having allowed this species to better respond to episodic but favorable changes to the habitat. Comparatively, in Kansas males reached sexual maturity in their second year; whereas, females became sexually mature in their third year in Kansas (Fitch 1999).

In Pennsylvania, parturition by the Redbelly Snake occurred during July-September (Hulse et al. 2001). The August peak in frequency of gravid females in Pennsylvania (Hulse et al. 2001) was the same month in which all post-partum Redbelly Snakes occurred at PNR. Female Redbelly Snakes at PNR were not gravid after July, which was also the case in northeastern Ohio (Meshaka et al. 2008b). In North Carolina, only 4% (2/50) gravid female appeared after July (Palmer and Braswell 1995), which was suggestive of a mid-summer end to parturition as in PNR Redbelly Snakes.

In Pennsylvania, the Common Garter Snake gave birth during August-September (Hulse et al. 2001), which were the two months with the highest frequencies of spent females during the June-September parturition season at PNR. In Manitoba, female Common Garter Snakes gave birth during August-September (Larsen et al. 1993).

Southward, parturition dates ranged July-September in North Carolina (Palmer and Braswell 1995) and May-November in the southern Everglades (Dalrymple et al. 1991). Although female Common Garter Snakes reproduced annually at PNR as they generally did in the rest of Pennsylvania (Hulse et al. 2001), this was not the case in northeastern Ohio (Meshaka et al. 2008b) or in Manitoba (Larsen et al. 1993).

Overall, the seasonal patterns associated with general activity and reproduction of PNR grassland snakes followed previously observed geographic trends of other populations. These interspecific and intraspecific differences detected at PNR were significant enough to underscore the importance of site-specific natural history data in formulating management plans for the resident species and their habitats. This is especially important in light of the methods conventionally used to maintain grasslands, such as burning and disking, that involve a physical disturbance capable of injuring or killing amphibians and reptiles. Seasonal timing plays an important role in successful grassland management programs such that the system is properly managed in a way that minimizes initial mortality that could be associated with treatment methods. These data revealed the vulnerability of snakes to grassland management tactics implemented from at least May through September when mating, gestating, surface movements, and parturition were prominent. Timing of grassland management activities should occupy the optimal seasonal window of management opportunity found between the end of intensely constrained snake activity in October and the beginning of winter weather that would hinder burning, disking, or mowing.

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