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Demographic Traits of an Eastern Gartersnake, *Thamnophis sirtalis sirtalis*, Population in Two Different Habitats

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Abstract.—We examined life history traits in Eastern Gartersnakes (*Thamnophis sirtalis sirtalis*) from two locations in an urban park in south-central Pennsylvania from 2015 to 2019. The combined sample differed most noticeably from other Pennsylvania populations only in mean clutch size and seasonal activity patterns. Within the park, however, many demographic traits differed between proximate sites. Population size, survivorship, and juvenile recruitment were lower, and catchability and likelihood of entry were higher on a xeric slope that leads to a highway than in a meadow. Variance in mean litter size was higher on the slope and only females from the slope exhibited a positive relationship between maternal body size and litter size. Broadly speaking, individuals from the park fit within many of the patterns associated with life history traits examined elsewhere in Pennsylvania, but the differences between sites reveal substantial variation in natural history responses in what otherwise might have been considered a single homogeneous site.

The Eastern Gartersnake (*Thamnophis sirtalis sirtalis*) is ubiquitous in Pennsylvania (Hulse et al. 2001; Meshaka and Collins 2009) and is abundant in Wildwood Park, a 94.5-ha county park in Harrisburg, Dauphin County, Pennsylvania (Wingert and Meshaka 2021). A previous mark-recapture study of snakes in the managed meadow of the park was conducted during 2004–2007 (Meshaka 2009). Since then, three ponds were created and encroaching trees were removed to maintain a larger and almost entirely open meadow. This study, conducted during 2015–2019, includes both the meadow and a sharp-angled dry southwest-facing shale embankment that received herbicide treatment and removal of exotic trees, resulting in a mosaic of mostly open habitat. Our aim was to determine the extent to which selected life history traits differed between sites and collectively differed from patterns associated with populations throughout the mid-Atlantic. Our interest in demographic responses in the Eastern Gartersnake stems from the dearth of ecological studies on this species despite its occurrence in many habitats in the eastern United States.

Methods

Study Site—As described in Meshaka et al. (2021), Wildwood Park (WP) is a 94.5-ha county park in Harrisburg, Dauphin County, Pennsylvania (40.315000, -76.885000). Approximately 60% of the park is comprised of a shallow artificial lake fed by Paxton Creek. A section of the Pennsylvania Canal runs along the western boundary of the park. The remainder of the park is primarily mixed deciduous forest.

A 0.50-ha artificial meadow, which slopes downward east to west, overlooks Wildwood Lake to the south and is surrounded on three sides by deciduous forest. This meadow was created in the 1970s to hold fill from nearby road construction, resulting in cleared trees and compressed soil. It is now maintained through annual mowing as an open habitat. In 2014–2015, three ponds were created in the meadow: West Pond (10.95 x 3.90 m, 11–38 cm depth), North Pond (6.68 x 2.43 m, 9–37 cm depth), and South Pond (7.60 x 2.04 m, 10–70 cm depth). The meadow comprises mixed grasses, patches of goldenrod (*Solidago* spp.), milkweed (*Asclepias* spp.) patches, Heath Aster (*Aster ericoides*), Wormwood (*Artemisia absinthium*), Dogbane (*Apocynum* sp.), and some Turtle Head (*Chelone* sp.) at the lower part of the slope (Fig. 1).

The shale-filled slope site, created in the 1970s during construction of the Rt. 322 entrance ramp, is a 133-m section of a southwest-facing 35° slope, 16 m from base

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Figure 1. Habitats in which Eastern Gartersnakes (*Thamnophis sirtalis sirtalis*) were surveyed in Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, from 2015 to 2019: Meadow view to the southeast point (left), and slope view to the northwest point (right). Photographs by E. Wingert.

to top. This ramp runs parallel to the top of the slope. Vegetation on the slope was mixed grasses, grape (*Vitis* sp.), Poison Ivy (*Rhus radicans*), patches of Wormwood, Great Mullen (*Verbascum thapsus*), Crown Vetch (*Securigera varia*), Tartarian Honeysuckle (*Lonicera tatarica*), Goldenrod (*Solidago* spp.), Catnip (*Nepeta cateria*), American Bittersweet (*Celastrus scandrens*), Canada Thistle (*Cirsium arvense*), Common Milkweed (*Asclepias tuberosa*), Wineberry (*Rubus phoenicolasius*), Heath Asters, grape (*Vitis* sp.), scattered Black Locust (*Robinia pseudoacacia*) saplings, Black Cherry (*Prunus serotina*) saplings, a large Honey Locust (*Gleditsia triacanthos*), and a Pin Oak (*Quercus palustris*) (Fig. 1).

Data collection.—We placed four 0.9 x 3.1-m corrugated metal cover boards in the meadow, two in the higher and drier southeastern end and two on the lower and wetter northwestern end, and another four 0.9 x 2.4-m corrugated metal cover boards along the slope, three mid-way up the slope and one at the top of the slope (0, 52, 75, and 133 m from the first cover board). All cover boards were placed in grassy spots with no woody vegetation so they would settle flat to the ground.

We visited the two sites 26 times during April–October 2015–2019, with 1–6 visits each month over the years of the study. When an Eastern Gartersnake was captured, we recorded sex and snout-vent length (SVL). Gravid females were gently palped to estimate litter size. Individuals with SVLs ≥ 24 cm were provided with a unique nine-digit AVID MUSICC Chip. Smaller individuals were marked with a single scale notch under the tail.

Data Analysis.—We used chi-square goodness of fit tests to ascertain differences in sex ratios of adults, F-tests prior to t-tests to compare mean adult body sizes between locations, and regression analyses to examine causative relationship between litter sizes and maternal body sizes. We estimated population size and survivorship by pooling all captures from both the meadow and slope and calculating apparent annual survival (Φ) and recapture rates (p) using open population Cormack-Jolly-Seber models (CJS; Lebreton et al. 1992) in Program MARK (White and Burnham 1999). We generated CJS models to examine whether Φ or p differed based on sex or time. We based model selection for all analyses on AICc (corrected AIC for small sample sizes) values, with lower values denoting greater parsimony (Burnham and Anderson 2002). We calculated population abundance for adults using POPAN parameterization of Jolly-Seber models (Jolly 1965; Seber 1965) in Program MARK (White and Burnham 1999). We then separated individuals between the meadow and slope site, and repeated the above calculations, comparing Φ, p, and PENT (probability of entry) between sites. PENT is a value used when calculating POPAN estimates that determine the probability of an unmarked individual entering the population.

Results

Adult body sizes.—Ten males and 33 females were marked in the meadow, and six males and 25 females were marked on the slope. Variances and means of adult body sizes did not differ significantly ($P > 0.05$) within sexes between sites. Combined, mean adult SVL of males (39.6 ± 5.3 cm SVL; 30.5–50.4 cm; n = 16) was 83.2% that of adult females (47.5 ± 5.3 cm; 39.2–56.4 cm; n = 58); the difference was significant (F-test, $P = 0.09$; t-test, $t = -3.6389$, $df = 72$; $P < 0.000$).

Adult sex ratios.—We detected no significant difference male:female sex ratios between locations ($X^2 = 0.1618$, $P > 0.05$). For all first-time captures at Wildwood Park, the male:female sex ratio was 0.28:1.00 and significantly female-biased ($X^2 = 22.4445$, $P = 0.000002$).

Juvenile recruitment.—Recruitment, as expressed as the percentage of young in the total sample of snakes captured for the first time, was markedly different between locations. On the slope, juveniles comprised 8.82% of all snakes captured.

In the meadow, having greater soil moisture and vegetation for cover, juveniles comprised 34.9% of initially captured snakes.

Clutch characteristics.—Mean litter sizes did not differ between sites (t-test, P = 0.29). However, variances of litter sizes differed significantly (F-test, F = 0.3738, P = 0.039) between the meadow (variance = 6.6) and the slope (variance = 17.70). Mean litter size of the combined samples was 12.4 ± 3.39 (5–18; n = 28). Mean and variance of SVL of gravid females from the slope (48.1 ± 4.5 cm; 40.8–53.6 cm; n = 12) were larger (t = 2.0836, df = 16, P = 0.054; F = 3.564, P = 0.012) than those from the meadow (45.1 ± 2.4 cm; 41.4–49.5 cm; n = 16). Mean SVL of all gravid females was 46.4 ± 3.7 cm (40.8–53.6 cm; n = 28). A positive relationship between maternal SVL and litter size was evident in females from the slope and for all females, but we detected no significant relationship in females from the meadow (Fig. 2).

Monthly movements.—During the April–October study period, snakes were bimodally active from the beginning of the study through September (Fig. 3). For all segments of the population, activity was greatest in June.

Mixed-sex aggregations of adult males and females.—Mixed-sex aggregations at Wildwood Park were evident in May (0.25), June (1.33), and September (0.20). On 24 September 2022, WEM and EW observed three males attempting to mate with a single female.

Parturition.—We detected gravid females during April–September with a peak in June, when we also found two spent females under covers (Fig. 4). The high incidence of gravid females in June and the simultaneous appearance of a

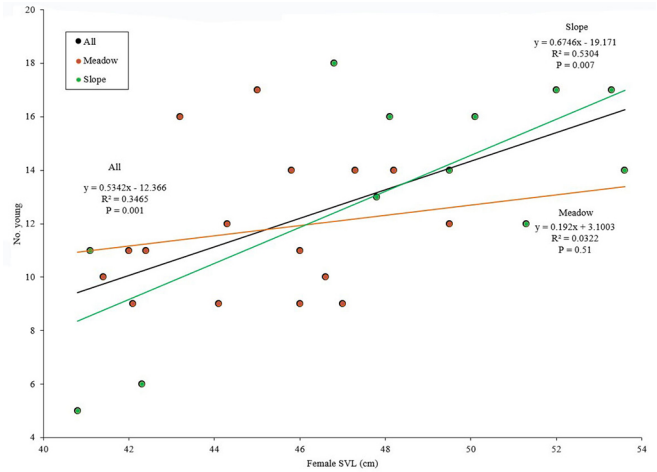

Figure 2. Relationship of litter size and female body size in the Eastern Gartersnake, *Thamnophis sirtalis sirtalis*, from Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2015–2019.

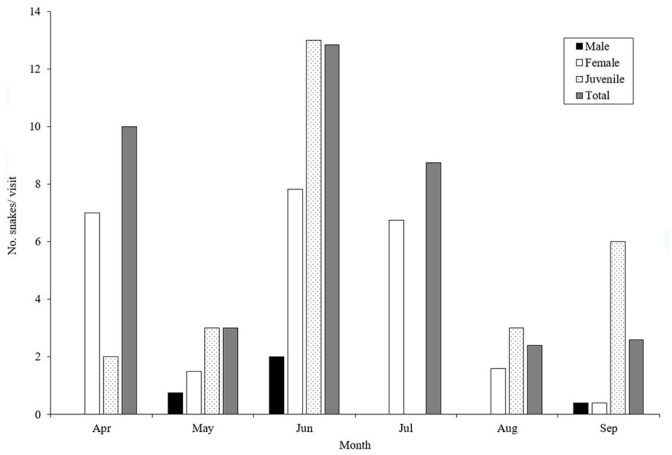

Figure 3. Monthly activity of the Eastern Gartersnake, *Thamnophis sirtalis sirtalis*, from Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2015–2019.

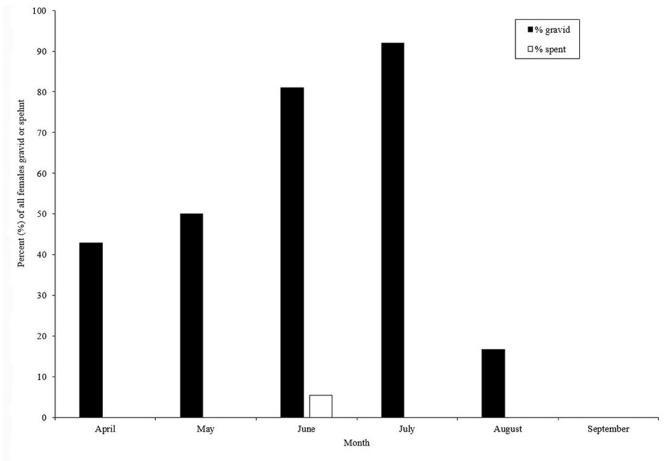

Figure 4. Monthly distribution of gravid and spent females of the Eastern Gartersnake, *Thamnophis sirtalis sirtalis*, from Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2015–2019.

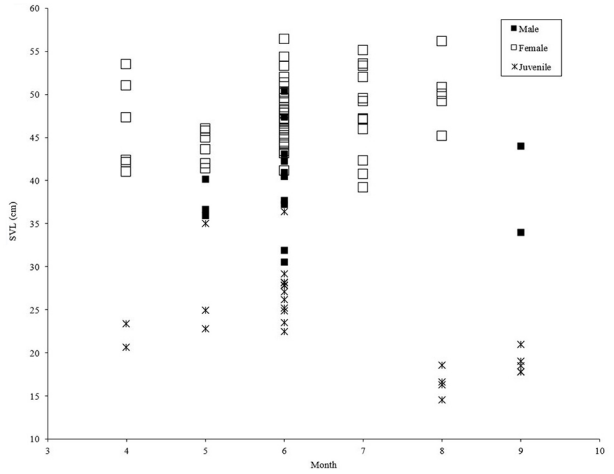

Figure 5. Monthly distribution of body sizes of the Eastern Gartersnake, *Thamnophis sirtalis sirtalis*, from Wildwood Park, Harrisburg, Dauphin County, Pennsylvania, during 2015–2019.

twice-captured spent female (22 and 29 June) was indicative of annual reproduction.

Growth to sexual maturity.—Young-of-the-year (YOY) did not appear under covers until August (Fig. 5). The smallest individual measured 14.6 cm SVL and was captured on 8 August. Growth to sexual maturity can be inferred by evidence of parturition in mid-June and estimated growth trajectories of presumed cohorts in each month (Fig. 5). Using these criteria, males could reach sexual maturity as early as June of the following year (their first birthday) or, if born later, no later than two months thereafter in August. Small sexually mature females seen in April (Fig. 5) were likely mature by September of the previous year at an age of 15 months if born in June.

Wounds, scars, and mortality.—Eight individuals were found with either physical damage or were found dead. Bobbed tails were found in two snakes, a male (43.1 cm SVL) from the meadow and a female (57.8 cm SVL) from the slope. Two males from the meadow were found with scars, 36.6 cm SVL with a scar above the cloaca on the left side and 26.0 cm SVL with a lateral scar on the body. Three females were found with blisters. In the meadow, the tail of a 54.3 cm SVL individual was partially covered in blisters. A 53.5-cm SVL snake was found with multiple old belly sores along the distal portions of ventral scales. On the slope, a 53.5-cm SVL snake had old blisters on its venter. An 18.6-cm SVL presumed YOY juvenile female was found dead under cover in the meadow on 23 August 2016.

Table 1. Number of individual Eastern Gartersnakes (*Thamnophis sirtalis sirtalis*) captured by sex, apparent survivorship (Φ), recapture probability (*p*), POPAN (population estimate ± 1 SE), and probability of an unmarked individual entering the population (PENT).

	n	Φ	*p*	POPAN	PENT
Female	85	0.25 ± 0.17	0.24 ± 0.21	85 ± 2.240	1.00
Male	23	0.47 ± 0.66	0.10 ± 0.17	23 ± >0.001	0.24

Table 3. Number of individual Eastern Gartersnakes (*Thamnophis sirtalis sirtalis*) by site, apparent survivorship (Φ), recapture probability (*p*), POPAN (population estimate ± 1 SE), and probability of an unmarked individual entering the population (PENT).

	Φ	*P*	POPAN	Pent
Meadow	0.71 ± 0.50	0.03 ± 0.04	669 ± 374	>0.001 ± 0.001
Slope	0.14 ± 0.05	1.00 ± 0.17	38 ± 2	1.00 ± 0.01

Table 2. Comparison of Cormack-Jolly-Seber models for apparent annual survival (Φ) and recapture rates (p) for the Eastern Gartersnake (*Thamnophis sirtalis*) in south-central Pennsylvania. Models differ in whether Φ and p are assumed to be constant (.), fully time-dependent (t), or differ between sexes (g).

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
Phi(t) p(g)	52.9721	0	0.19708	1	5	1.2912
Phi(g) p(t)	52.9860	0.0139	0.19571	0.9931	5	1.3051
Phi(g) p(g)	54.6812	1.7091	0.08385	0.4255	3	7.3725
Phi(.) p(.)	55.2472	2.2751	0.06318	0.3206	2	10.0598
Phi(t) p(t)	57.4780	4.5059	0.02071	0.1051	6	3.5433

Table 4. Comparison of Cormack-Jolly-Seber models for apparent annual survival (Φ) and recapture rates (p) for Common Gartersnakes (*Thamnophis sirtalis*) in south-central Pennsylvania. Models differ in whether Φ and p are assumed to be constant (.), fully time-dependent (t), or differ between sexes (g).

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
Phi(g) p(g)	72.1558	0	0.27010	1	4	11.2993
Phi(.) p(g)	72.7838	0.6280	0.19731	0.7305	3	14.0948
Phi(t) p(g)	73.0056	0.8498	0.17660	0.6538	6	7.6773
Phi(.) p(.)	74.3801	2.2243	0.08882	0.3288	2	17.8148
Phi(t) p(.)	74.7069	2.5511	0.07543	0.2793	5	11.6378
Phi(.) p(t)	74.7650	2.6092	0.07327	0.2713	5	11.6959
Phi(g) p(.)	75.5274	3.3716	0.05005	0.1853	3	16.8383
Phi(g) p(t)	75.7828	3.6270	0.04405	0.1631	6	10.4545
Phi(t) p(t)	76.9661	4.8103	0.02438	0.0903	6	11.6378

Population sizes, survivorship, and recapture probability.—Females had lower Φ but higher *p* than males (Table 1). Results of model testing suggested that both Φ and *p* varied by time and group (Table 2). We did not expect that overall captures would vary with time, as seasonality can affect detection. With the assumption that Φ includes both emigration and mortality, the lower Φ value and higher PENT value in females suggests that females are consistently moving into and out of the population.

Comparing sample sites, snakes in the meadow had higher Φ values and lower *p* values. Estimated population size in the meadow was much higher than on the slope (Table 3), whereas PENT values were considerably higher on the slope (Table 3). In the most parsimonious model, Φ and *p* varied between sites (Table 4). PENT and Φ values calculated for the meadow and the slope suggest higher rates of movement into and out of the slope site than the meadow site.

Discussion

We compared eleven life history traits between the two sites in Wildwood Park. Adult body sizes of both sexes were similar between sites. Likewise, mean clutch size did not differ between sites; however, variance in clutch size was higher in females inhabiting the slope, and a significant maternal body size effect on clutch size was observed only in females on the slope. Population size, survivorship, and juvenile recruitment was lower on the slope, whereas recapture rate and probability of entry was higher. The combination of demographic responses by the Eastern Gartersnake to the two sites speaks to what appears to be a population sink on the slope. We suggest that the structurally more open and drier slope might be poorer habitat for juveniles due to greater visibility to predators and perhaps limited moisture, especially in shaly xeric portions of this habitat. Secondarily, food might have been less available, which could contribute to low recruitment and the wide variation in clutch size in that habitat when compared to the more predictable source of earthworm and anuran prey in the lusher meadow and its ponds.

Life history traits affecting demography in the Eastern Gartersnake in Pennsylvania were generally similar among various sites and study dates with some notable exceptions. For example, mean body sizes and sex ratios of adult Eastern Gartersnakes were generally similar across sites, especially those where the Northern Black Racer (*Coluber constrictor constrictor*) was absent. In an earlier study in the Wildwood Park meadow and a nearby residential area, mean adult SVL of males was 41 cm and that of females was 50–51 cm with respective male:female SVL ratios of 83.0% and 81.0% (Meshaka 2009). At Letterkenny Army Depot (LEAD) in south-central Pennsylvania (Meshaka and Delis 2014), mean male SVL (38.9 cm) was similar to that in this study, but females at LEAD were very large (mean SVL = 64.3 cm) in Northern Black Racer-rich areas and somewhat less large (mean SVL = 54.1 cm) in areas where that predator was absent. Elsewhere at LEAD, one male and 34 adult females (mean SVL = 45.8 cm) were captured (Hughes et al. 2018). In southwestern Pennsylvania grasslands, mean adult male SVL was 39.6 cm and that of females 47.3 cm. The respective male:female SVL ratio was 84.0% (Meshaka 2010). Likewise, a relatively constant pattern in adult body sizes and body size ratios between sexes was evident among Pennsylvania sites other than those of Meshaka and Delis (2014). To that end, the presence of racers appears to select for fewer and larger individuals of other snake species (Kjoss and Litvaitis 2001; Meshaka et al. 2009; Dallas et al. 2021). In Pennsylvania as a whole, mean body sizes of adults were small in males (mean = 33.8 cm) and females (mean = 43.9 cm) (Hulse et al. 2001).

In an earlier study in the Wildwood Park meadow and a nearby residential area, respective sex ratios were 0.23:1.00 and 0.22:1.00 (Meshaka 2009). The sex ratio at LEAD also favored females (0.43:1.00) (Meshaka and Delis 2014). Elsewhere in LEAD, only one adult male was captured in a study in which 34 females were captured (Hughes et al. 2018). Among adults in southwestern Pennsylvania grasslands, males were outnumbered by females 0.27:1.00 (Meshaka 2010). As in the case of adult body sizes, sex ratios of sites other than those of Meshaka and Delis (2014) were relatively constant.

Juvenile recruitment is highly variable among other Pennsylvania sites: 3.73% (Meshaka and Delis 2014), 9.15% (Meshaka 2010), and 28.6% (Hughes et al. 2018). These differences indicate measurable responses in a demographic trait, the causes of which could include predator pressure, food availability, or habitat suitability, the latter two of which we suspect are responsible for differences between sites in this study.

Clutch sizes in this study averaged lower than in many sites elsewhere in Pennsylvania and mirrored the findings of a significant relationship between litter size and maternal body size. Along a tow path at Wildwood Park, mean litter size was 19.6 young with no significant association between litter size and female body size (Meshaka and Morales 2016). However, the relationship was significant when an extremely large female was removed from the sample, her small litter size due perhaps to food limitation or reproductive senescence. Larger female body size alone explained the larger litter size in LEAD (mean = 16.4 young) than in southwestern Pennsylvania (mean = 13.0 young), and litter sizes of both samples co-varied with female body size (Meshaka and Delis 2010). Also at LEAD, gravid females averaged 54.3 cm SVL and produced an average of 15.3 young annually. The relationship between litter size and maternal body size was positive and significant (Meshaka and Delis 2014). Along wetlands at LEAD, mean litter size was 12.3 with no significant association between litter size and female body size (Hughes et al. 2018). Larger

clutches averaging 19.5 young were produced accompanied by a significant association between litter size and female body size among snakes from the Susquehanna River in downtown Harrisburg (Meshaka et al. 2012). In Pennsylvania generally, litter sizes averaged 22.4 young (Hulse et al. 2001); however, these latter two values and that of Meshaka and Morales (2016) were estimated by counts from dissected females.

The modality and peaks of monthly activity in the Pennsylvania populations of the Eastern Gartersnake vary among sites and years. For example, in an earlier study at Wildwood Park, most gartersnakes were seen in May, followed by July (Meshaka 2009). Seasonal activity was bimodal (June and August) during April–October surveys in LEAD (Hughes et al. 2018). However, elsewhere in LEAD and during other years than those sampled by Hughes et al. (2018), seasonal activity in LEAD was unimodal during April–September, peaking in June and July (Meshaka and Delis 2014). Activity was unimodal at a residential site near Harrisburg, where gartersnake activity peaked in July, followed by a rapid decline in activity (Meshaka 2009). In downtown Harrisburg, visually-encountered basking or moving individuals were seen during March–September. Seasonal activity was unimodal, peaking in April for both sexes, with most young found in May (Meshaka et al. 2012). At Powdermill Nature Reserve (PNR) in southwestern Pennsylvania, seasonal activity during May–September surveys was also unimodal, peaking in July (Meshaka 2010). In Pennsylvania generally, activity peaks in May and begins to taper off in September (Hulse et al. 2001). In northwestern Pennsylvania, activity peaks and modality varied between years, unimodal with a July peak in one year, followed by bimodal activity that peaked in May and August the following year (Gray 2014). In Gray's (2014) study, peak activity of adults and juveniles also varied between years.

Seasonal distribution of mixed-sex aggregations is typically bimodal in this species in Pennsylvania. Mixed-sex groupings were detected in May (n = 2), June (n = 2), and September (n = 1) at LEAD (Meshaka and Delis 2014), and a September mating was observed at Fort Hunter, a riverside park in Harrisburg, Dauphin County (Meshaka et al. 2020). Mixed-sex aggregations in southwestern Pennsylvania occurred during May–September, with most records in June followed by August–September (Meshaka 2010). In Pennsylvania generally, mating takes place in April and May and to a lesser extent in September and October (Hulse et al. 2001).

Females in this study conformed to the June–August parturition season found in other Pennsylvania populations. The highest incidence of gravid females was in July at both sites studied by Meshaka (2009). Spent females were detected in August at Wildwood Park and detected in July and especially in August in a residential area near Harrisburg (Meshaka 2009). Most gravid females from south-central Pennsylvania were detected in June and none past July (Meshaka and Delis 2014; Hughes et al. 2018). In southwestern Pennsylvania, females were gravid during May–August, the lowest frequency of which was in August (Meshaka 2010). Females were spent during June–September, with the highest frequencies of spent females in the latter two months (Meshaka 2010). In downtown Harrisburg, all young were produced by August (Meshaka et al. 2012), and females were gravid through July in northeastern Pennsylvania (Gray 2014). Thus, June–August comprises most of the birthing season of these Pennsylvania sites.

Generally speaking, appearance of YOY and presumed growth rates vary only slightly among sites in Pennsylvania. Both traits in this study overlapped those of Wildwood Park (Meshaka 2009), downtown Harrisburg (Meshaka et al. 2012), LEAD (Meshaka and Delis 2014; Hughes et al. 2018), and southwestern Pennsylvania (Meshaka 2010). Exceptionally, males of the Meshaka et al. (2012) study might have matured within a few months of birth. In northeastern Pennsylvania, YOY were first encountered in July (Gray 2014).

Frequencies of tail loss are uncommonly reported for Pennsylvania populations of Eastern Gartersnakes. In our populations, tail-loss frequencies were lower than those of either sex from Pennsylvania generally (Hulse et al. 2001) or northwestern Pennsylvania (Gray 2015). Among injuries, an Eastern Garter snake from southwestern Pennsylvania was cut by the blade of a brush hog (Meshaka 2009).

The Eastern Gartersnake, despite its ubiquity in Pennsylvania (Hulse et al. 2001), has only recently been the subject of ecological study in the Commonwealth. Studies such as this can serve to quantify variability in demographic responses by this species to natural and human-mediated habitat perturbations, and might generate a measure of predictability in understanding responses to a rapidly changing environment.

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