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Roadside Habitat Use by the Endemic Short-headed Gartersnake (*Thamnophis brachystoma*) in Northwestern Pennsylvania, USA

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***Abstract.*—The Short-headed Gartersnake (*Thamnophis brachystoma*) has one of the most restricted ranges of any snake species in the United States, with approximately 90% of the total distribution within northwestern Pennsylvania, USA. Although recent surveys indicate that the species can be locally abundant, evidence suggests an overall decrease in population size, which is attributed to habitat loss due to succession of previously open-canopied communities. Because of their affinity for open-canopied habitats, areas adjacent to road construction are frequently used by Short-headed Gartersnakes. A better understanding of the habitat requirements of the species is a necessary first step toward the development of species-specific conservation strategies. In 2010, we conducted surveys for Short-headed Gartersnakes and associated habitat sampling at 39 roadside sites in northwestern Pennsylvania. We detected Short-headed Gartersnakes at 18 of 39 sites surveyed. Based on regression analysis, distance to permanent water, canopy cover, and rock cover best predicted species detection. Sites where the species was detected were closer to permanent water sources, had more rock cover, and less canopy cover than sites where it was not detected. Our results suggest that roadside sites with appropriate conditions can provide Short-headed Gartersnake habitat. The use of roadside sites by this species may prove to be logistically and financially appealing for managing habitat and monitoring populations.**

Key Words.—canopy cover; conservation; cover rock; disturbance; endemism; logistic regression

Introduction

The small size and secretive habits of many squamates, particularly snakes, make them some of the least-understood vertebrates with respect to ecological requirements. The lack of such information often results in snake taxa being overlooked in terms of conservation assessment and implementation (Böhm et al. 2013). Many snake species have been identified as priority species for conservation, nonetheless, a lack of knowledge regarding the basic ecology and life-history requirements limits the development of conservation strategies (Gibbons et al. 2000; Reading et al. 2010; Böhm et al. 2013).

The Short-headed Gartersnake (*Thamnophis brachystoma*; Fig. 1) is listed as a Species of Greatest Conservation Need (Pennsylvania Game Commission and Pennsylvania Fish & Boat Commission [PGC-PFBC] 2015) in Pennsylvania, USA, and presently has a global rank of G4 and a state ranking of S4 (Pennsylvania Natural Heritage Program. 2015. Species List of Amphibians and Reptiles of Conservation Concern in Pennsylvania. Pennsylvania Natural Heritage Program. Available from http://www.naturalheritage.state.pa.us/Species.aspx [Accessed 14 December 2015]). Despite its listing as a species of Least Concern on the International Union for the Conservation of Nature (IUCN) Red List, the Short-headed Gartersnake warrants conservation concern because it has one of the most restricted ranges of any snake in the United States. The species is endemic to northwestern Pennsylvania and adjacent southwestern New York (Ernst and Ernst 2003) in the U.S. and occurs primarily on the Northern Unglaciated Allegheny Plateau, with populations also occurring within the Southern Unglaciated Allegheny Plateau, Western Glaciated Allegheny Plateau, and Erie and Ontario Lake Plain (U.S. Forest Service. 2008. Travel routes for Region 1. U.S. Forest Service, Region 1, Regional Office Engineering, Missoula, Montana. Available from http://www.fs.fed.us/r1/gis/thematic_data/TravelRoutesR1.htm [Accessed 1 December 2014]). The landscapes of these ecoregions are extensively forested and include rounded hills, low mountains, and narrow valleys. Approximately 90% of the global population of Short-headed Gartersnakes resides in northwestern Pennsylvania (Price 1978; Hulse et al. 2001), and although recent surveys indicate that Short-headed Gartersnakes are locally abundant in parts

Figure 1. Short-headed Gartersnake (*Thamnophis brachystoma*) from Forest County, Pennsylvania, USA. (Photographed by Julie Mibroda).

of their range (Timothy Maret, unpubl. report), the lower density of the species at historically occupied locations suggests an overall population decline (Richard Bothner, unpubl. report). A better understanding of the habitat of Short-headed Gartersnake habitat requirements is necessary to guide efforts to conserve or restore quality habitat and thus promote long-term viability of populations of this potentially vulnerable species.

Short-headed Gartersnakes are usually observed in close proximity to water (Swanson 1952; Klingener 1957; Asplund 1963; Ernst and Ernst 2003), and only rarely found in deep woodlands (Hulse et al. 2001). In fact, it has been suggested that habitat loss due to forest succession on previously disturbed sites may be driving population declines (Richard Bothner, unpubl. report). A general description of the habitat of the species includes areas of limited canopy dominated by low vegetation (e.g., old fields, wetland edges, roadsides) where objects such as rocks, logs, or human litter (e.g., corrugated tin, plywood) provide cover (Klingener 1957; Ernst and Gotte 1986; Hulse et al. 2001; Ernst and Ernst 2003). Beyond these anecdotal habitat descriptions, no surveys designed to understand how microhabitat characteristics influence habitat use by Short-headed Gartersnakes have been conducted. As such, the factors that contribute to the restricted range of this species remain unknown and science-based habitat guidelines are unavailable to land managers.

Roads are generally not considered landscape features that benefit wildlife (Forman and Alexander 1998). However, areas adjacent to roads can provide habitat opportunities for some species, and thus potentially mitigate some of the adverse impacts of road networks (Bennett 1991; Underhill and Angold 1999). Sites adjacent to roads may provide important habitat for the Short-headed Gartersnake because roads often follow water courses and have areas characterized by reduced tree canopy and the presence of rocks and ground vegetation. Moreover, road corridor management of mowing and herbicide application maintains the open habitats used by Short-headed Gartersnakes throughout the active season. To examine the influence of habitat characteristics on the detection of Short-headed Gartersnakes at roadside sites, we conducted Short-headed Gartersnake and habitat surveys at roadside sites in northwestern Pennsylvania and modeled habitat features at sites where the species was detected and undetected. Based on previously published accounts (Klingener 1957; Ernst and Gotte 1986; Hulse et al. 2001; Ernst and Ernst 2003), the discriminating features may include availability of cover objects, ground level vegetation, tree canopy cover, and proximity to permanent water source. Information obtained from this study provides an important first step toward developing a science-based conservation strategy for this range-limited species.

Materials and Methods

Study area.—We surveyed 39 roadside sites across eight counties of northwestern Pennsylvania, USA: Clearfield, Elk, Erie, Forest, Jefferson, McKean, Venango, and Warren. The counties selected for this study encompassed a significant proportion (approximately 80%) of the global range of the species (Conant and Collins 1998). Survey sites ranged in size from 0.01–1.45 ha. We chose sites based on results from previous herpetological surveys (Timothy Maret, unpubl. report) or because of their apparent potential to support Short-headed Gartersnakes. We considered a site suitable for inclusion in this study when at least one rock measuring $\geq 20 \times 30$ cm was clearly visible and not embedded deep in the ground (to provide sufficient space between the rock and ground that could accommodate snakes). Surveyed sites had rock cover that varied from covering the entire site to only several rocks scattered across the site (Fig. 2). Some surveyed sites included other types of cover objects (e.g., woody debris and drift fence), but inclusion in the study was based on rock cover presence only. Most (n = 35) of the study sites were located on public roadside rights-of-way and four sites were on privately owned land. Thirty-six sites were adjacent to paved roads and three were located near unpaved access roads. All sites were associated with disturbances created by road construction or maintenance and were located within 5 m of a road.

Short-headed Gartersnake surveys.—We surveyed each of our 39 sites three times, once each during three different sampling periods: May, June, and September/October 2010. We conducted surveys during the active season of the species, and we avoided July and August when Short-headed Gartersnake activity levels are reported to decrease (Hulse et al. 2001) and

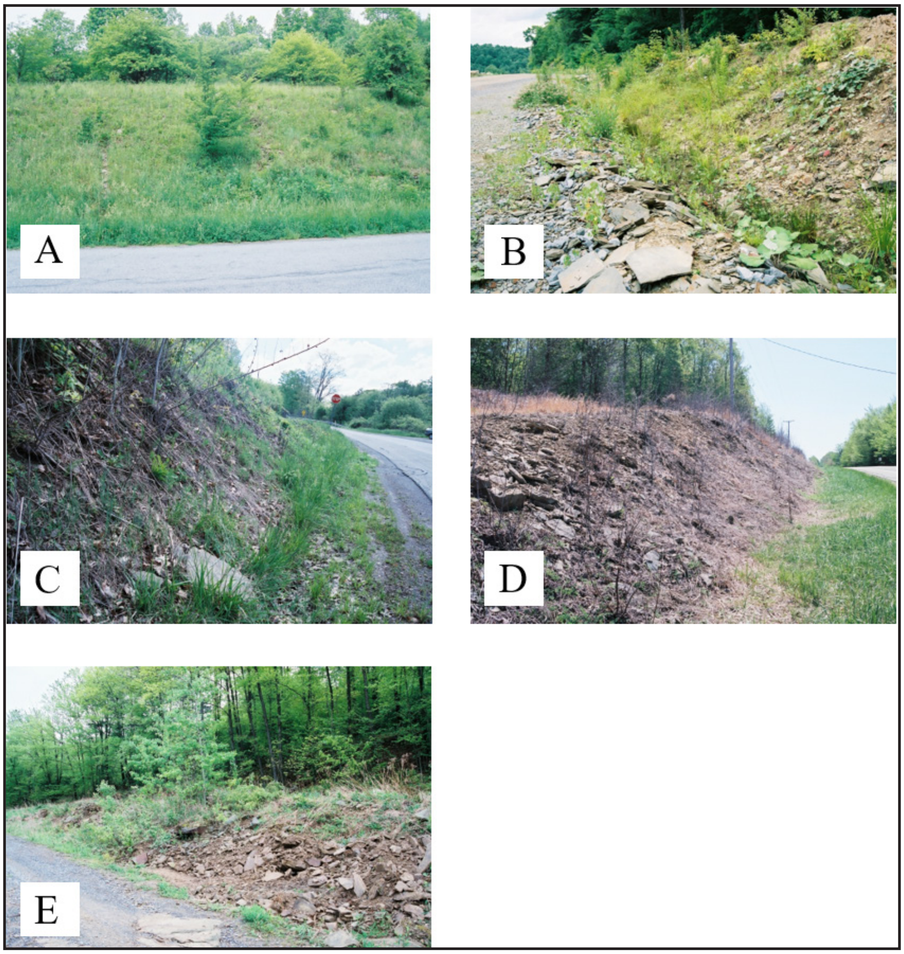

Figure 2. Short-headed Gartersnake (*Thamnophis brachystoma*) roadside habitat in: (A) McKean County, (B) Jefferson County, (C) Forest County, (D) McKean County, and (E) Clearfield County of Pennsylvania, USA. (Photographed by Julie Mibroda).

detection probability decreases (Julie Mibroda, pers. obs.). During surveys, we turned cover objects within each site, and replaced each to its original position whenever possible. When we captured Short-headed Gartersnakes, we weighed them to the nearest 0.5 g with a spring scale, measured them to the nearest 0.5 cm with a flexible measuring tape, noted their overall condition, photographed them, and released them immediately post-processing. We measured the length, width, and thickness of rocks under which we found Short-headed Gartersnakes. We also noted the presence and identity of all other snake taxa observed. Surveys were time-constrained so that the same search effort per unit area was applied to each site, to ensure a consistent level of survey effort across all study sites.

Habitat surveys.—At each study site, we quantified 10 habitat features: percentage rock cover, percentage bare ground, percentage herbaceous plant cover, percentage coarse woody debris (CWD) cover, frequency of cover rocks, number of shrubs, number of saplings, number of trees, percentage canopy cover, and Euclidean distance to nearest permanent water source. We estimated the percentage of ground covered by rocks, bare ground, herbaceous plants (i.e., grass, forbs), CWD, and frequency of cover rocks within ≥ 30 plots measuring 1 m^2 and spaced every 4 m along parallel transects at each study site. Transects were spaced 4 m apart, started within the site on either the right or left side of the site nearest the road (oriented while facing the site, side was randomly chosen), and ran either parallel or diagonal to the road (direction was randomly chosen). For frequency of cover rocks, we only considered rocks that measured at least the minimum length and width, and no greater than the maximum thickness of those under which we observed Short-headed Gartersnakes (≥ 11 cm long × ≥ 11 cm wide × ≤ 9 cm thick); each 1 m^2 plot that contained at least one rock fitting these measurements was counted within each site. For CWD, we only considered objects that were > 2.5 cm diameter (Harmon et al. 1986). We also estimated percentage canopy cover directly above each 1 m² plot using an ocular tube. We quantified number of shrubs (> 0.5 m tall), number of saplings (< 10 cm diameter at breast height [dbh]), and number of trees (≥ 10 cm dbh) within five 5-m radius plots that we randomly distributed across each site. We used ArcGIS 10.1 and a raster-based landcover dataset (National Agriculture Imagery Program [NAIP]. Available from https://www.arcgis.com/home/item.html?id=0ecb05ec9e0540d3a201c4ef9d2aee88 [Accessed 14 December 2014]) to measure the distance from each the centroid of each site to the nearest permanent water source (i.e., stream, pond, lake).

Data analysis.—To characterize the observed counts of Short-headed Gartersnakes relative to other snakes observed in the community, we compared the maximum detections at each location for the four most commonly observed snakes. For this analysis, we excluded absences for all other species. Our comparisons were performed as a mixed-effects regression model based on a negative binomial distribution (glmer.nb in package lme4; R v. 3.1.2; R Development Core Team 2016). For this model, we considered each species a fixed effect and we included location as a random effect.

We developed logistic regression models to identify roadside habitat characteristics that best predicted detection of Short-headed Gartersnakes. We modeled species detection with the general linear model (glm) function using a binomial distribution (glmer.nb in package lme4; R v. 3.1.2; R Development Core Team 2016). We analyzed species detection among study sites using presence data for Short-headed Gartersnakes at each site along with 10 habitat variables judged as potential predictors of species detection.

To reduce the chance of producing over-parameterized models, we limited models to a maximum of three variables. We sought to reduce the chance of multicollinearity in our models by calculating pairwise Pearson's correlation values among our variables. If the correlation between two variables exceeded 0.7, then we removed one of the highly correlated variables from consideration in the models. Prior to developing our models, we standardized each covariate to have a mean of 0 and standard deviation of 1 to allow for comparison of the relative effect size among variables. We compared models using Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002; package AICcmodavg). We used the cumulative Akaike weights for the models containing each variable to rank variables according to their Relative Importance (RI; Arnold 2010). For each variable, we used model averaging to estimate regression coefficients and standard error (Burnham and Anderson 2002). We followed the recommendations of Arnold (2010) and used 85% confidence intervals to evaluate statistical significance.

We performed two diagnostic tests to evaluate our highest ranked models. We evaluated the discriminatory power of our highest ranked model using a Receiver Operating Characteristic (ROC) curve based on our model building dataset. We measured the area under the curve (AUC; package pROC; Program R). An AUC value = 1 would indicate a model perfectly predicted roadside sites used by Short-headed Gartersnakes, whereas a value of 0.5 would indicate the model was equivalent to random guessing (Fielding and Bell 1997). We tested for overdispersion by calculating the variance inflation factor (residual deviance over the residual degrees of freedom; $\hat{c}$) of the most parameterized model in the competing model set. Values for $\hat{c}$ that are approximately 1 indicate that there is no evidence of overdispersion (MacKenzie et al. 2006).

Results

Short-headed Gartersnake surveys.—We recorded 99 Short-headed Gartersnake detections across 18 of 39 sites surveyed during three sampling periods in 2010. We did not mark snakes so re-sightings of the same individual may have occurred among sampling periods. In addition to Short-headed Gartersnakes, we detected seven additional snake species: Northern Ring-necked Snake (*Diadophis punctatus edwardsii*; n = 117; 28 sites), Eastern Gartersnake (*Thamnophis sirtalis sirtalis*; n = 37; 17 sites), Northern Red-bellied Snake (*Storeria occipitomaculata occipitomaculata*; n = 36; 20 sites), Eastern Milksnake (*Lampropeltis triangulum triangulum*; n = 8; four sites), Northern Watersnake (*Nerodia sipedon sipedon*; n = 5; four sites), Eastern Ratsnake (*Pantherophis alleghaniensis*; n = 3; two sites), and Smooth Greensnake (*Opheodrys vernalis*; n = 3; two sites). The average observed count per site per sampling period for Short-headed Gartersnake ($\bar{x}$ = 3.17) was similar to that of Northern Ring-necked Snake ($\bar{x}$ = 3.14; Coefficient Estimate (CE) = 0.0089, SE = 0.200; t = 0.045, df = 43, P = 0.964) and greater than Eastern Gartersnake ($\bar{x}$ = 1.65; CE = -0.642, SE = 0.259; t = -2.480, df = 43, P = 0.013) and Northern Red-bellied Snake ($\bar{x}$ = 1.50; CE = -0.731, SE = 0.252; t = -2.902, df = 43, P = 0.004).

Habitat.—Of the 10 habitat variables we quantified (Table 1), one variable (percentage herbaceous cover) was highly correlated with two other variables (percentage rock, r = -0.768; percentage bare ground, r = -0.729), and was thus excluded from the analysis. Our regression analyses resulted in a candidate model set of 130 models. The highest ranked model contained three

Table 1. Habitat variables collected at 39 roadside sites in northwestern Pennsylvania, USA, in 2010, to investigate differences between sites where Short-headed Gartersnakes (*Thamnophis brachystoma*) were detected from sites where the species was not detected.

	Occupied (n = 18)				Unoccupied (n = 21)			
Habitat Characteristic	Mean	(SE)	Min	Max	Mean	(SE)	Min	Max
Rock (%)[a]	18.37	4.18	0	75	11.45	2.36	0	95
Bare ground (%)[a]	10.21	1.57	0	50	13.29	3.72	0	100
Vegetation (%)[a]	70.15	4.49	0	100	74.39	5.04	0	100
Coarse woody debris (%)[a]	0.99	0.35	0	30	0.88	0.51	0	50
Canopy cover (%)[a]	1.41	0.69	0	50	10.91	4.63	0	100
Frequency of cover rock[a]	2.56	0.38	0	6	1.82	0.29	0	4
No. of shrubs[b]	1.67	0.40	0	4	2.41	0.43	0	8
No. of saplings[b]	0.78	0.26	0	3	0.36	0.16	0	2
No. of trees[b]	2.89	0.84	0	10	2.73	0.61	0	13
Distance to water (m)	397.22	131.87	0	1930	1598.73	695.39	47	15250

[a]Characteristic collected within 1 m^2 plots; [b]Characteristic collected within 5-m radius plots

variables and was not overdispersed ($\hat{c}$ = 1.11). When averaged across models, three variables (distance to water, percentage canopy cover, and frequency of cover rock) had 85% confidence intervals that did not overlap with zero (Table 2). The three variable model appeared to be a good predictor of Short-headed Gartersnake detection (AUC = 0.85; 95% CI = 0.72–0.98). The remaining six variables appeared less important (RI ≤ 0.17) and all had confidence intervals that overlapped with zero (Table 2). Sites where we detected Shorthead Garter Snakes were closer to permanent water sources (Distance to water CE = -2.95, SE = 1.52, 85% CI = -5.14, -0.76), had lower percent canopy cover (Canopy cover CE = -0.95, SE = 0.47, 85% CI = -1.62, -0.28), and had a higher frequency of cover rock (Frequency of cover rock CE = 0.71, SE = 0.44, 85% CI = 0.07–1.35) than sites where the species was not detected (Table 2).

Discussion

Our study is the first to quantify the influence of habitat features on the detection of Short-headed Gartersnakes. Our results support previous anecdotal observations that suggested the species typically inhabits open-canopied sites containing cover objects within a few hundred meters of water (Wozniak and Bothner 1966; Ernst and Gotte 1986; Hulse et al. 2001). The primary goal of our study was to determine the extent to which Short-headed Gartersnakes used roadside sites and to identify habitat features that most influenced species detection at such sites. Distance to a permanent water source was the habitat attribute that best explained the detection of Short-headed Gartersnakes at our study sites. Specifically, the species was more likely to be found at roadside sites that were closer to a permanent

Table 2. Relative importance values and model-averaged estimates of scaled regression coefficients from logistic regression models describing the detection of Shorthead Garter Snakes at roadside sites in northwestern Pennsylvania. Habitat data were collected at 39 sites surveyed in northwestern Pennsylvania, USA, in 2010.

Parameter	Relative Importance Value	Coefficient Estimate (CE)	CE Standard Error	CE Lower Conf. Interval 85%	CE Upper Conf. Interval 85%
Distance to water	0.78	-2.95	1.52	-5.14	-0.76
Canopy cover (%)	0.67	-0.95	0.47	-1.62	-0.28
Frequency of cover rock	0.30	0.71	0.44	0.07	1.35
Coarse woody debris (%)	0.17	0.53	0.44	-0.11	1.17
Rock (%)	0.16	0.49	0.48	-0.19	1.18
No. of saplings	0.16	0.45	0.44	-0.18	1.03
No. of shrubs	0.15	0.43	0.41	-0.16	0.15
No. of trees	0.14	-0.41	0.39	-0.98	0.15
Bare ground (%)	0.10	-0.14	0.48	-0.83	0.55

water source. Sites where Short-headed Gartersnakes were detected and undetected were on average 397 and 1,598 m from a permanent water source, respectively. One possible explanation behind this relationship may be related to differences in the availability of prey across a soil moisture gradient. Earthworm populations, a major prey item for Short-headed Gartersnakes (Gray 2010), are known to be affected by soil moisture (Hallatt et al. 1992). Despite our gap in knowledge regarding the causal mechanism behind the positive relationship between the detection of Short-headed Gartersnakes and distance to water, we suggest that conservation efforts intended to create or enhance habitat for this species should target areas close (< 400 m) to a permanent water source.

Canopy cover was another habitat feature that was an important estimator of Short-headed Gartersnake detection at roadside sites, whereby canopy cover was lower at sites where the species was detected compared to sites where it appeared to be absent. Throughout much of the range of the Short-headed Gartersnake, the availability of early successional habitats characterized by reduced canopy cover has decreased dramatically due to forest succession (Trani et al. 2001). Forest succession on previously disturbed sites has been suggested as a factor driving the decline of many disturbance-dependent species in the eastern U.S. (Askins 2001). Canopy cover has been cited as an important factor affecting habitat quality for other reptile species (Pringle et al. 2003; Webb et al. 2005; Pike et al. 2011), and decreased canopy cover is positively correlated with reptile abundance and diversity (Pike et al. 2011; Nicoletto 2013). Roadways through extensively forested areas of the range of Short-headed Gartersnakes create canopy gaps that allow for the development of early successional or edge habitat that is otherwise limited in availability.

Rock cover was the final habitat feature that our analysis revealed to be important for explaining the detection of Short-headed Gartersnakes at roadside sites. Cover objects are important to many snake species, as they provide security from predators and as sites that facilitate thermoregulation (Gregory 2004; Charland and Gregory 1995). Previous investigators have anecdotally noted an apparent close association between Short-headed Gartersnake detection and the availability of cover objects (Klingener 1957; Ernst and Gotte 1986; Hulse et al. 2001; Ernst and Ernst 2003). A study of radio-tagged gartersnakes (*T. sirtalis* and *T. elegans*) in Canada concluded that the species were associated with areas characterized by high levels of cover and gravid females were primarily restricted to rocky areas that were relatively rare on the study site (Charland and Gregory 1995). Indeed, availability of thermally suitable rocky cover is a limiting resource to imperiled snakes species elsewhere (Pringle et al. 2003). We suggest it is possible that suitable rocky cover may be limited throughout much of the highly-forested range of the Short-headed Gartersnake, and thus, roadside sites with open canopies and abundant rocky cover may be important to the reproductive success and population persistence of the species.

Nevertheless, neither the presence of a species nor patterns of habitat use are indicative of habitat quality (Van Horne 1983). Indeed, the demography of these roadside populations should be carefully evaluated and compared to other populations to ensure that roadside habitats do not represent population sinks because of road mortality (Pulliam 1988). Road mortality may have strong effects on snake population dynamics and roadside habitats could potentially inflate the impacts of road mortality on survival of adult Short-headed Gartersnakes (Row et al. 2007). Snake population growth (λ) is highly sensitive to changes in adult mortality, a life stage we anticipate to be most heavily impacted by potential road mortality (Altwegg et al. 2005). While a demographic study on Short-headed Gartersnakes will be critical for the long-term conservation of this species, there is no doubt that the roadside habitats studied here provide early successional habitat for this range-limited species.

Our study only examined diurnal habitat use of Short-headed Gartersnakes during the active portion of its life cycle. As such, the species may, and likely does, use other cover types (e.g., closed-canopy forest) during other parts of the day or phases of its annual life cycle. For example, a comparison of radio-tagged and non-radio-tagged Eastern Pine Snakes (*Pituophis melanoleucus*) in New Jersey revealed that radio-tagged individuals spent equal amounts of time in forested and disturbed habitats, whereas non-radio tracked snakes were detected almost exclusively (> 90% of observations) in disturbed habitats (Burger and Zappalorti 1988). Our study focused solely on open, rocky, disturbed roadside habitats; this is not assumed to represent the entirety of the habitat requirements of Short-headed Gartersnakes. For example, the habitat requirements of the species as listed in the 2015 Pennsylvania Wildlife Action Plan include riparian old fields and meadows with grasses, sedges, low herbaceous growth, and early successional perennials (PGC-PFBC 2015). Nonetheless, our findings contribute to a growing body of literature that identifies the need to maintain adequate amounts of open-canopied/early successional habitats as a component of forested landscapes to benefit many species of wildlife (Askins 2001; Mitchell et al. 2006; Gilbart 2012).

Although the total count of Short-headed Gartersnakes was not the highest observed across our study sites, when the species was detected it occurred at relatively high numbers compared to most other snake species. The Short-headed Gartersnake is described as social (Hulse et al. 2001; Jellen 2010), and the number of detections during this study is similar to observations during a previous effort to evaluate populations, whereby the species was uncommon across most of the landscape but demonstrated the capacity to occur at high abundances locally (Timothy Maret, unpubl. report). Certainly, the detection of eight species of snakes, particularly two that are Species of Greatest Conservation Need in Pennsylvania (Short-headed Gartersnake and Smooth Greensnake), at these roadside sites demonstrates the value of maintaining these open-canopied habitats throughout the landscape.

The results of our study represent an important first step to understanding the habitat needs of the Short-headed Gartersnake. Our analysis revealed that roadside sites with abundant cover rocks and minimal canopy cover (< 10%) that are within 400 m of a permanent water source provide habitat for this range-limited species of conservation concern. The manipulation of canopy cover through the periodic removal of shrubs, saplings, and trees (Webb et al. 2005) at roadside sites with sufficient rocky cover and close proximity to water may be an effective conservation strategy for the Short-headed Gartersnake. An alternative to manipulating canopy cover, albeit potentially more costly, would be to create new rocky habitat patches in existing open areas near water. We suggest that canopy reduction over existing rocky sites or the creation of new areas with cover rock could be incorporated into mitigation plans of future road construction projects in the region. Additionally, efforts to increase the availability of Short-headed Gartersnake habitat should be closely monitored to evaluate the response of Short-headed Gartersnakes and to modify management prescription should it be warranted.

We recommend future monitoring should use a repeated survey design to estimate detection probability, occupancy, and abundance of Short-headed Gartersnakes in several potential habitat types. Additionally, studies should quantify home range size and movement patterns of the species beyond roadside sites, to more completely characterize its habitat requisites. Finally, a demographic study of this species, particularly one comparing dynamics in roadside habitats to non-roadside patches would be valuable to ensure that roadside habitats support sustainable population growth.

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