Evaluating Snake Density Using Passive Integrated Transponder (PIT) Telemetry and Spatial Capture–Recapture Analyses for Linear Habitats

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Abstract.—Many snake species are elusive and difficult to study in field settings. As such, little is known about their population ecology despite conservation needs for many species. Advances in field techniques and statistical methods can improve our understanding of snake ecology. We used passive integrated transponder (PIT) telemetry to track *Nerodia sipedon* (Northern Watersnakes, *n* = 94) and *Regina septemvittata* (Queensnakes, *n* = 119) in six low-order streams in central Kentucky, USA from June to October 2016. We assessed snake density, spatial scale of detection, and detection probability using PIT tag relocations and spatial capture–recapture methods for linear habitats. Specifically, we modeled population density as a function of individual stream and land cover type, spatial scale of detection as a function of sex, and detection probability as a function of sex and time-varying covariates. Individual streams were a better predictor of snake density than land cover type; density estimates ranged from 6 ± 3 *N. sipedon*/km (mean ± standard error) to 107 ± 17 *N. sipedon*/km and 6 ± 5 *R. septemvittata*/km to 63 ± 10 *R. septemvittata*/km. Female *R. septemvittata* had a larger spatial scale of detection (55 ± 4 m) than male *R. septemvittata* snakes (40 ± 4 m). Spatial scale of detection did not differ between sexes for *N. sipedon* (females: 40 ± 4 m; males: 35 ± 3 m). The combination of PIT telemetry and spatial capture–recapture analyses can effectively estimate population densities and other population parameters for snakes and other reptiles and amphibians associated with linear habitats.

Precise estimates of animal population sizes are critical for management and conservation action. Yet, calculating population sizes can be difficult because of the secretive nature of some species and the logistics required to sample individuals (Witmer, 2005; Mazerolle et al., 2007; Muñoz et al., 2016). Estimating snake population sizes is notoriously challenging because of their cryptic coloration, limited activity periods, their use of structurally complex habitats, and other aspects of their natural histories (Mazerolle et al., 2007; Durso and Seigel, 2015; Ward et al., 2017). Ultimately, it can be difficult to obtain sufficient snake recaptures or detections for most population estimation methods (e.g., capture–mark–recapture or occupancy analyses) because of low detection rates (Attum et al., 2009; Sewell et al., 2012; Böhm et al., 2013; Ward et al., 2017). Nevertheless, snake populations are experiencing myriad threats (Böhm et al., 2013; Lorch et al., 2016; Todd et al., 2017; McKenzie et al., 2019) and population size estimates are necessary to accurately determine conservation status and management needs.

Recent advances in field technologies and analytical approaches offer the potential to improve investigations of snake populations. Passive integrated transponder (PIT) tags have long been used for snake population studies (e.g., Camper and Dixon, 1988; Gibbons and Andrews, 2004). These tags are inserted subcutaneously and are coded with a unique number that is used to identify the individual (Gibbons and Andrews, 2004). An improvement in this method includes PIT telemetry; through the use of an antenna and portable reader, an individual's unique identification and spatial location can be recorded beyond tactile range (Connette and Semlitsch, 2012; Oldham et al., 2016). Individual detections and spatial locations collected via PIT telemetry provide data necessary for spatial capture–recapture (SCR) analyses (Muñoz et al., 2016; Efford, 2018). SCR analyses require spatial coordinates of traps or detections, capture history of marked individuals, a habitat mask or state space, and covariates if desired. These data can come from traps or active searching, but PIT telemetry allows detections of snakes that would not otherwise be seen (e.g., under large rocks, in thick vegetation) and results in more detections than traditional methods (Oldham et al., 2016). Some SCR models incorporate specific landscape structures that better represent the interactions between the animals and their environment (Raabe et al., 2014; Efford, 2017). These models estimate population densities, spatial scale of detection, and detection rates with limited bias and decent precision even for species with low detection rates and elusive traits (Kéry et al., 2011; Blanc et al., 2013; Head et al., 2013; Royle et al., 2014). Thus, the combination of PIT telemetry and SCR offers the potential to provide valuable ecological information regarding snake population densities and other aspects of their ecology.

In this study, we used PIT telemetry and SCR to determine population densities, spatial scale of detection, and detection rates of two stream-dwelling natricine species: *Nerodia sipedon* (Northern Watersnakes) and *Regina septemvittata* (Queensnakes). Specifically, to illustrate the utility of this approach, we asked three questions. (1) Do population densities vary across our study sites? (2) Does sex influence the spatial scale of detection? (3) What factors (e.g., sampling covariates) influence detection probabilities of snakes? We used an SCR method adapted for linear habitats, which models movement as it occurs within the stream (Efford, 2017); the adaptation is particularly beneficial as water snakes and other herpetofauna commonly reside in linear habitats such as streams.

Materials and Methods

Study Sites.—We sampled snakes at six streams within the Kentucky River basin (Fig. 1). These streams were in four central Kentucky counties (Fayette, Jessamine, Madison, and Woodford). Three streams (Glenns, Little Hickman, and Tates) had primarily (i.e., >50%) forested catchments, and three (Elias, Elkhorn, and Hickman) had catchments dominated (i.e., >30%) by suburban land cover. Streams ranged from first to third order (Strahler, 1957). Streams were typically shallow (<0.5 m deep), with
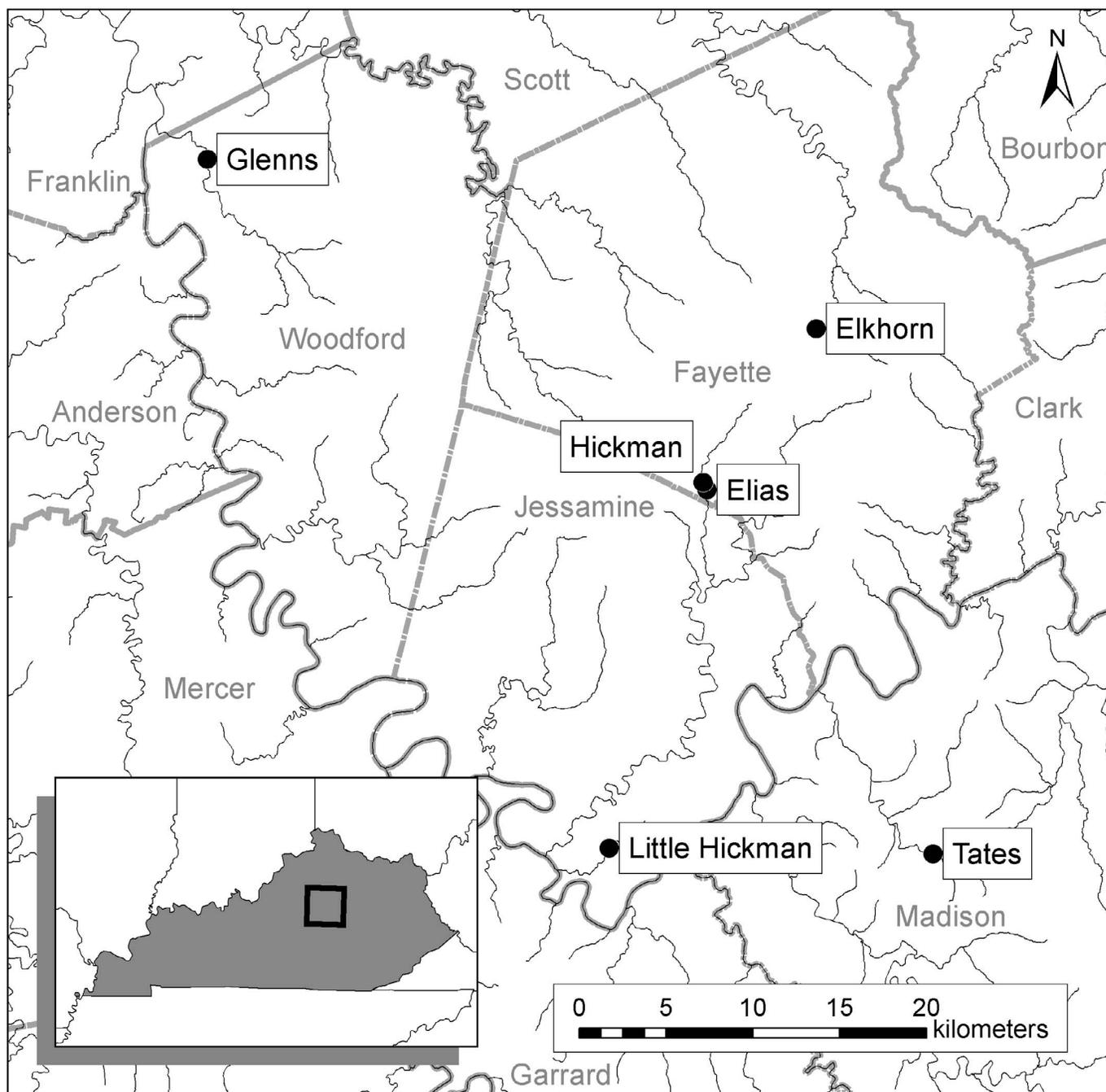
Fig. 1. Location of six streams surveyed for *Nerodia sipedon* and *Regina septemvittata* in central Kentucky, USA.

exposed bedrock and rocky sections. Stream banks contained rocks and vegetation, with trees lining the banks at most locations.

Snake Surveys.—At each site, we performed 4–16 visual surveys for snakes within transects (569 ± 20 m, mean length ± standard error [SE]; range: 196–1,021 m) between 8 March and 3 June 2016. We brought captured snakes to the lab to measure, sex, and insert PIT tags. We implanted snakes with 134.2-kHz 12.5-mm PIT tags (Biomark HPT12) using the Biomark MK10 Implanter (Boise, Idaho, USA). PIT tags were inserted subcutaneously along the posterior third of the venter anterior to the cloaca. Snakes were released within 48 h at the capture location. Three streams (Elias, Hickman, and Little Hickman) were sampled for snakes and surveyed in previous years. Marked snakes from previous years

were only included in the analysis if detected during the surveys in March–June 2016 and during the PIT telemetry surveys in June–October 2016 (see below).

We surveyed stream transects using PIT telemetry every 7–11 d (mean: 8.1 ± 0.1 d) from 6 June to 12 October 2016 for a total of 16 surveys per stream. We walked the established transects at each stream and used a Biomark HPR Plus portable reader and BP portable antenna to locate snakes. Specifically, we used the antenna (PIT tag detection range 30–43 cm) to scan large rocks, ledges, vegetation, and other locations that snakes could inhabit along the entire length of each transect on both sides and the center of the stream. If a snake was detected, the PIT tag number and global positioning system (GPS) coordinates were automatically recorded in the reader (Oldham et al., 2016). We
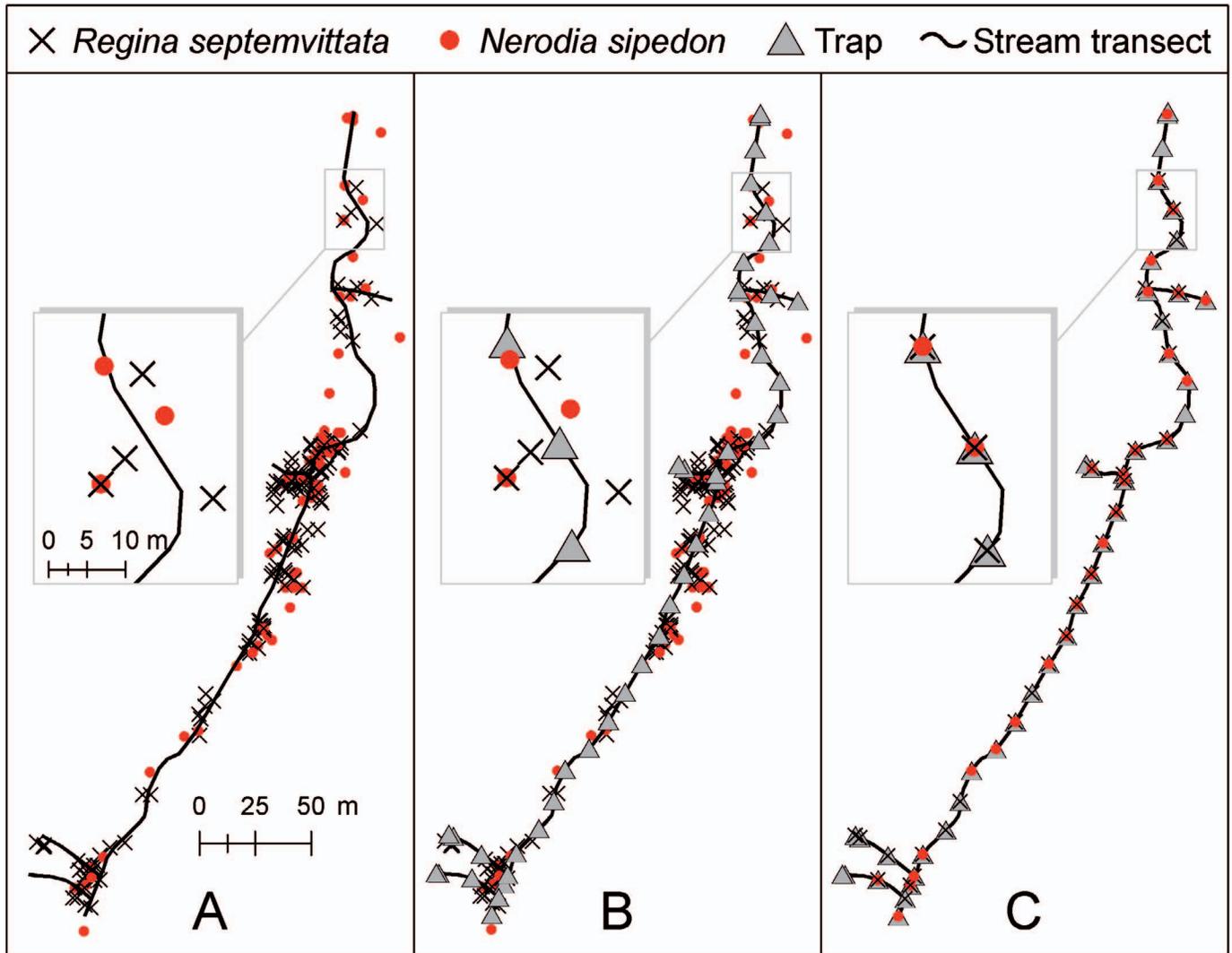
Fig. 2. Location of snake detections for *Nerodia sipedon* and *Regina septemvittata* along a stream (A), creation of "traps" placed approximately every 15 m in ArcGIS (B), and snapping detections to the trap locations in ArcGIS (C). Data are shown for one stream in Kentucky, USA.

searched the detection location to visually confirm the snake's presence. We recorded environmental covariates that may influence detection rates including water temperature (recorded before each PIT telemetry survey), day of year, number of days since last rain event, and the amount of rain accumulation between surveys (Weather Underground, 2016).

Data Analysis.—We used the secrlinear package in R (R Core Team, 2018), which was developed to use SCR methods in linear habitats (Efford, 2017) to assess density, spatial scale of detection, and detection of both snake species. This analysis requires detections at specific points, rather than a search–encounter approach like our PIT telemetry surveys. Thus, we created trap locations at 15-m intervals along each stream and at the end of each stream in ArcGIS version 10.4.1 (ESRI, 2016; Efford, 2017). We chose 15 m as traps must be close enough for some individuals to visit multiple traps while ensuring that the distance between traps was farther than the GPS error (± 3 m). We tested models with 30-m intervals between traps to investigate the effect of trap spacing on our estimates. We snapped the locations of each snake detection to the nearest trap (Fig. 2; Efford, 2017).

Before addressing our research questions, we removed several snakes from the data set to meet closure assumptions of the model. First, we only included snakes that were detected during the PIT telemetry surveys in our analyses; individuals captured and marked before PIT telemetry during visual encounter surveys (or in previous years, see above) were removed as they may have moved from our transects. More important, our methods did not detect unmarked individuals, so our density values are underestimates as our population was restricted to marked individuals. Second, we removed individuals that were detected at the same location without visual encounters on multiple consecutive occasions as these detections may be the result of a dropped or expelled PIT tag (e.g., Roark and Dorcas, 2000) that sank to the stream bottom rather than moving regularly (Bubb et al., 2006). In addition, one *N. sipedon* was removed from the analyses because it was predated by a *Chelydra serpentina* (Snapping Turtle). Thus, we retained all detections that were represented by visual encounters, movement upstream, position changes (e.g., from riparian zone to center of stream), or in locations that precluded visual observation (e.g., under large rocks) when detected on nonconsecutive occasions.

TABLE 1. Covariates and model selection information from spatial capture–recapture analyses of *Nerodia sipedon* and *Regina septemvittata*. We checked all detection variables for correlation and collinearity. The process started with a global model (density ~ stream; spatial scale of detection ~ sex; and detection ~ sex + day of year + water temperature + days since last rain + rain accumulation). We retained sex in all models for both spatial scale of detection and detection. All possible subsets of the four other detection covariates were run, and the covariates included in the top model based on the highest likelihood (exp[−0.5 × ΔAIC$_c$]) were used in all remaining models. We ran three density models (stream, land cover type, and a null model) and any models with a likelihood ≥0.125 were considered supported models.

		Model selection results	
Parameter	Covariate	*N. sipedon*	*R. septemvittata*
Density	Stream	Supported	Supported
Density	Land cover type	Not supported	Not supported
Density	Null	Not supported	Not supported
Spatial scale of detection (σ)	Sex	In all models	In all models
Detection (g0)	Sex	In all models	In all models
Detection (g0)	Day of year	In top model	In top model
Detection (g0)	Water temperature	Not in top model	In top model
Detection (g0)	Days since last rain	In top model	In top model
Detection (g0)	Rain accumulation	Not in top model	In top model

The first steps in the analysis included preparing the linear mask, creating a trap location data frame, and generating capture histories. First, the linear mask can be generated from a point shapefile of the stream locations, which we created in ArcGIS (Fig. 2; ESRI, 2016). This component can have covariates regarding stream characteristics; we used land cover type and stream. The linear mask, or state space, is designed to encompass the activity centers of any animals detected within the sampled area (Royle et al., 2014; Efford, 2018). The spatial scale of detection parameter (σ) × 4 is one way to estimate the distance needed to buffer the sampling area. Preliminary analyses indicated that σ was 33–40 m for *N. sipedon* and 40–55 m for *R. septemvittata*. Therefore, we buffered our start and end locations of the streams or stream branches by 220 m to account for the largest of these preliminary values; this buffer, combined with our sampling transect length, represented our state space. Instances where the stream ended and became nonhabitat were not buffered or considered state space. Second, the trap location data frame consists of GPS coordinates and unique trap identification numbers of each trap. We did not include any trap-specific covariates, although those can also be incorporated in this modeling framework. We specified trap usage in another matrix, indicating which sites were surveyed on each occasion. Covariates measured each time a site was surveyed can be included in a separate data frame as time-varying covariates; we recorded day of year, water temperature, days since last rain, and rain accumulation between surveys. Each of these was modeled as linear predictors of detection probability. Third, the capture history contains one row per individual per detection, with the PIT tag number, occasion, trap identification number, and individual covariates. Sex was the only individual covariate we used. We assigned sex to snakes if there were 75% or more visual encounters of the same sex or if there were more adult verdicts of a particular sex than juvenile verdicts of the other sex. Only seven snakes had inconclusive recordings of sex (*N. sipedon*, four snakes; *R. septemvittata*, three snakes).

We modeled each species separately and incorporated sex using a hybrid mixture model that can account for snakes whose sex was uncertain. The model calculated density, spatial scale of detection (σ), and detection probability (g0; Efford, 2017). We fit σ using a half-normal distribution and used this parameter to derive an estimate of home range size. If movement is normally distributed around the home range center, σ × 3.92 (1.96 for the two standard deviations from the mean × two directions) represents an approximate 95% home range assuming an unbranched section of stream (Efford, 2017). In a dendritic section of stream, the estimated home range size will be larger as the home range extends the same distance in all possible directions from the home range center (Efford, 2017). We also assessed g0, which refers to the capture probability during a single occasion at a trap placed at the center of the individual's home range, and g0 decreases as distance from the home range center increases.

We checked assumptions regarding covariates and performed model selection to choose supported models (Table 1). We assessed correlations and collinearity in our time-varying covariates and did not include covariates with correlations >0.7 or variance inflation factors >3 (Zuur et al., 2009). All continuous covariates were standardized (Schielzeth, 2010). We compared all combinations of day of year, water temperature, days since last rain, and rain accumulation to determine the model with the lowest Akaike's information criterion corrected for small sample sizes (AIC$_c$; Hurvich and Tsai, 1989). For all initial detection models, sex was included as a covariate for σ and g0, and stream was included for density (Table 1). We chose the best detection model, maintaining sex as a covariate for σ and g0, and ran three models with density as a function of stream, land cover type (forest or suburban), and a null density model (Table 1). We used the likelihood of a model given the data (exp[−0.5 × ΔAIC$_c$]) with a cutoff of ≥0.125 to select supported models (Burnham and Anderson, 2002). We assessed the significance of sex based on the beta coefficients. If the 95% confidence intervals overlapped zero for the coefficient of sex on σ or g0, then sex was not considered significant for that term.

RESULTS

We PIT tagged 172 *N. sipedon* and 176 *R. septemvittata* between 8 March and 3 June 2016. Of these, we detected 94 *N. sipedon* and 119 *R. septemvittata* between 6 June and 12 October 2016. During our 16 surveys, we detected individual *N. sipedon* an average of 2.5 ± 0.2 times (mean ± SE) and individual *R. septemvittata* 2.7 ± 0.2 times (range: one to eight detections for *N. sipedon* and one to nine detections for *R. septemvittata*).

Our initial model selection approach for detection covariates determined that day of year and days since last rain affected both *N. sipedon* and *R. septemvittata* detections. Rain accumula-
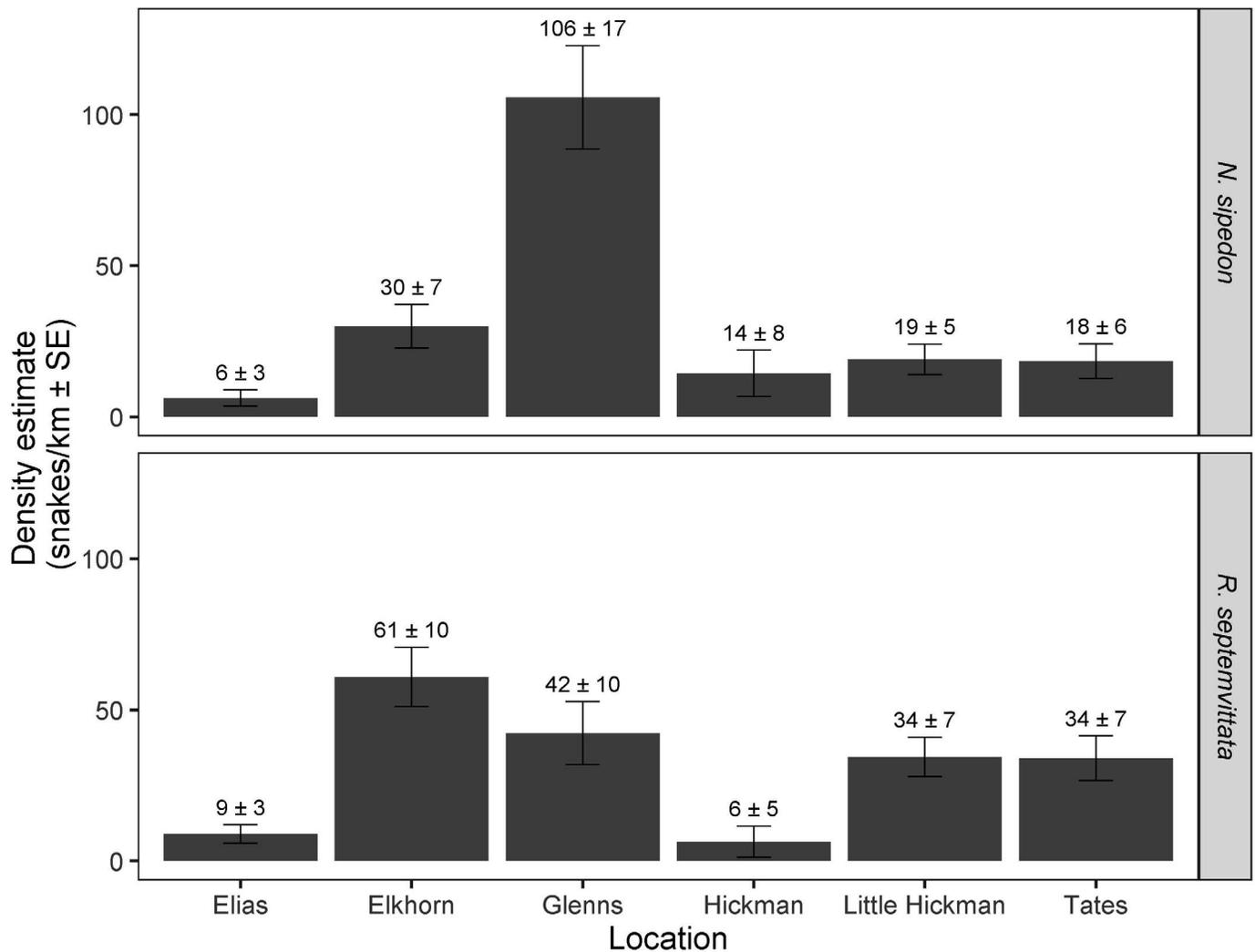
FIG. 3.   Density estimates for *Nerodia sipedon* and *Regina septemvittata* in six central Kentucky streams. Results were based on trap spacing of 15 m between traps.

tion and water temperature were also included in the best detection model for *R. septemvittata* (Table 1). We used these detection covariates to select supported density models. Individual streams were a better predictor of snake density than land cover type or the null model, with likelihoods of <0.001 for the next best models for both species. Density estimates ranged from 6 ± 3 *N. sipedon*/km to 107 ± 17 *N. sipedon*/km and 6 ± 5 *R. septemvittata*/km to 63 ± 10 *R. septemvittata*/km (Fig. 3). The beta parameter for the effect of sex on the spatial scale of detection overlapped zero for *N. sipedon*, indicating no significant difference between the sexes, with female snakes having a spatial scale of detection of 40 ± 4 m and male snakes having a spatial scale of detection of 35 ± 3 m (Table 2). Female *R. septemvittata* had larger spatial scales of detection (55 ± 4 m) than males (40 ± 4 m, Table 2). These values correspond to approximate home ranges of 156 ± 15 m for female *N. sipedon,* 138 ± 13 m for male *N. sipedon,* 216 ± 16 m for female *R. septemvittata,* and 156 ± 14 m for male *R. septemvittata.* We found no effect of sex on detection rates for either species (Table 2). Detection rates for both species decreased over the course of the season and with fewer days since last rain (Table 2; Fig. 4). *Regina septemvittata* detection rates decreased with increased rain accumulation between

surveys and with higher water temperatures (Table 2; Fig. 4). Using a trap spacing of 30 m instead of 15 m did not alter our conclusions (Appendix 1).

DISCUSSION

Our approach of PIT telemetry and SCR analyses for linear habitats resulted in estimates of population density, spatial scale of detection, and detection rates for two snake species. Our estimates of population densities ranged from 6 to 107 *N. sipedon*/km and 6 to 63 *R. septemvittata*/km and were within the lower portion of the densities observed for both *N. sipedon* (4–281 *N. sipedon*/km) and *R. septemvittata* (1–263 *R. septemvittata*/km) in previous studies (Branson and Baker, 1974; Hebrard and Mushinsky, 1978; Bekker, 2007; Cecala et al., 2010). Published estimates of density for other natricine snakes were also similar to the range of our estimated densities, with 1–55 snakes/km for six different *Nerodia* or *Regina* species (Hebrard and Mushinsky, 1978; Mills et al., 1995), with larger densities for Lake Erie Watersnakes (*N. sipedon insularum,* 10–400 snakes/km, King, 1986; King et al., 2006). The imperiled Copperbelly Watersnake (*N. erythrogaster neglecta*) had lower densities of 2.0–5.4 snakes/km (Lacki et al., 2005). However, snake densities estimated in previous studies often had high standard errors because of low

TABLE 2. Beta coefficients, standard errors (SE), and 95% confidence intervals (CI) for covariates affecting detection (g0) and spatial scale of detection (σ) parameters in spatial capture–recapture analyses for *Nerodia sipedon* and *Regina septemvittata*. Covariates were deemed significant (*) if the 95% confidence intervals did not overlap zero. Results were based on trap spacing of 15 m between traps.

Species	Parameter	Covariate	Beta	SE	Lower CI	Upper CI
N. sipedon	Detection (g0)	Sex	0.36	0.21	−0.05	0.77
N. sipedon	Detection (g0)	Days since last rain*	0.18	0.06	0.05	0.30
N. sipedon	Detection (g0)	Day of year*	−0.57	0.08	−0.72	−0.41
N. sipedon	Spatial scale of detection (σ)	Sex	−0.16	0.13	−0.42	0.10
R. septemvittata	Detection (g0)	Sex*	0.36	0.18	0.01	0.71
R. septemvittata	Detection (g0)	Rain accumulation	−0.12	0.07	−0.25	0.01
R. septemvittata	Detection (g0)	Days since last rain*	0.16	0.07	0.02	0.30
R. septemvittata	Detection (g0)	Water temperature*	−0.14	0.06	−0.26	−0.01
R. septemvittata	Detection (g0)	Day of year*	−0.56	0.06	−0.68	−0.44
R. septemvittata	Spatial scale of detection (σ)	Sex*	−0.30	0.11	−0.53	−0.08

detection rates or did not account for imperfect detection (Hebrard and Mushinsky, 1978; King, 1986; Lacki et al., 2005; Bekker, 2007); most of our estimates had relatively small standard errors and incorporated imperfect detection of individuals. However, we caution that our population densities are underestimates as we limited the population available for detection to the snakes marked during the March–June visual surveys (i.e., we did not mark new snakes during PIT telemetry surveys). As such, our results are specific to the marked population of snakes and we are uncertain as to the relationship
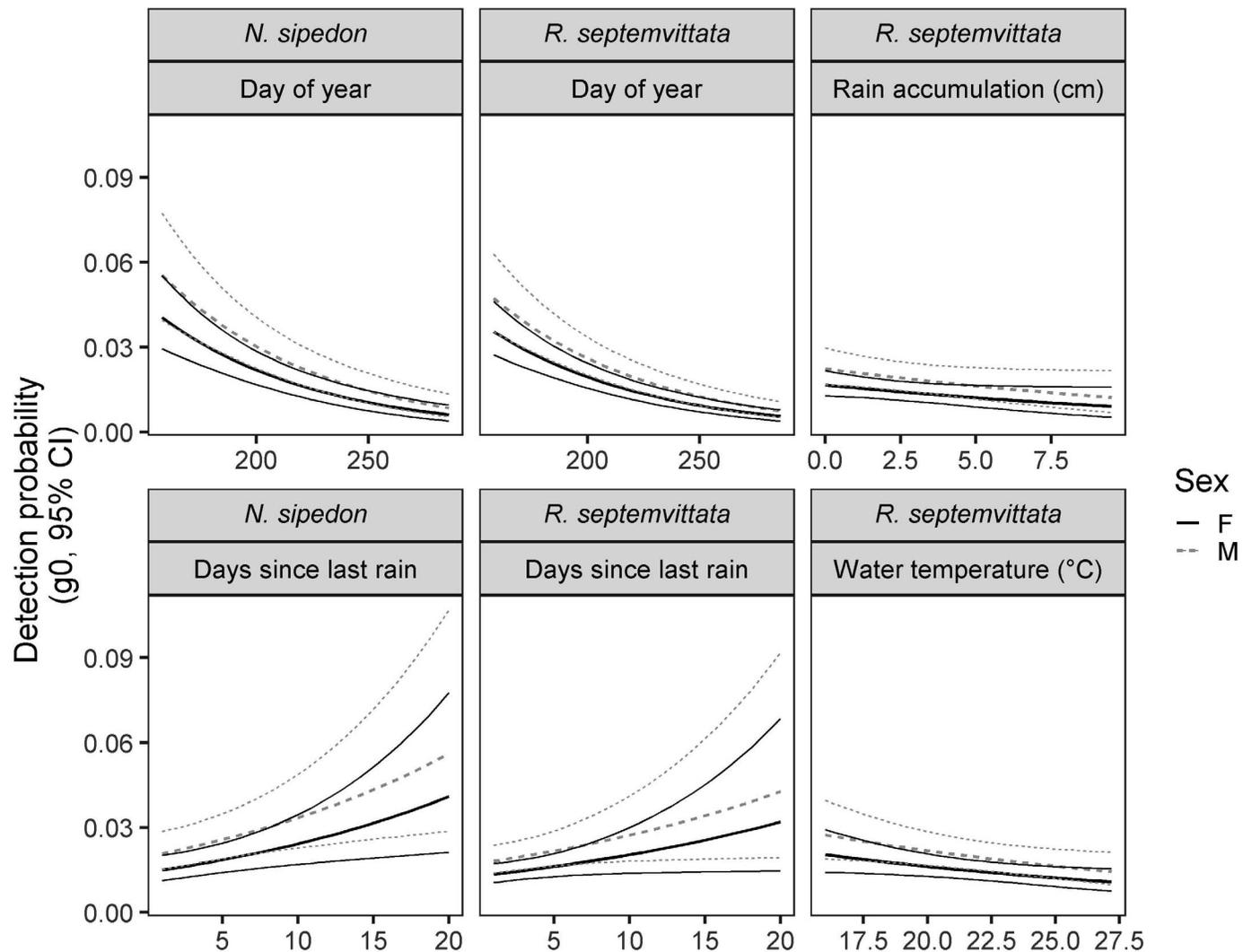

FIG. 4. Detection probabilities of *Nerodia sipedon* and *Regina septemvittata* on the basis of days since last rain, rain accumulation, day of year, and water temperature in central Kentucky between 6 June and 12 October 2016. Solid black lines indicate mean and 95% confidence intervals for female snakes; dashed gray lines indicate mean and 95% confidence intervals for male snakes. Differences among sexes were not significant for *N. sipedon*. Rain accumulation and water temperature were not included in the best model for *N. sipedon* and are not shown. Results were based on trap spacing of 15 m between traps.

between our marked population and the overall population of snakes present at our sites. Nonetheless, we believe our approach can be useful to track changes in population density over time, make comparisons among study sites, and ascertain whether conservation actions are necessary.

Patterns in density of animal populations are often driven by habitat features. We found that density estimates varied among streams, as stream was a better predictor than land cover types within stream catchments. Stream characteristics such as connectivity and permanence are known to affect snake densities (Robertson and Weatherhead, 1992; Lacki et al., 1994; Mills et al., 1995; Pattishall and Cundall, 2009). For example, *R. septemvittata* in Kentucky were found only in permanent streams (Branson and Baker, 1974), and connectivity with permanent water bodies resulted in higher densities for two *Nerodia* species (Lacki et al., 1994; Attum et al., 2007). Although we had only six study sites, our results also suggest that stream order may influence density; we sampled one first-order stream (Elias, Fig. 1) and this site supported a lower density of both species than the other streams we surveyed, which were all second- or third-order streams. We note that future investigations or extensions to our modeling approach could include incorporating habitat features. Habitat features affecting snake density include prey availability, vegetation density, canopy cover, basking locations, and slope along stream bank (Branson and Baker, 1974; Hebrard and Mushinsky, 1978; Mills et al., 1995; Pattishall and Cundall, 2009), all of which may be easily measured in the field. Understanding the relationship between habitat features and density could assist with management efforts (Shoemaker et al., 2009).

Our analyses also improved our understanding about the spatial scale of detection and estimated home range sizes for *N. sipedon* and *R. septemvittata*. We found that female *R. septemvittata* had larger home ranges than males, although no differences in home range size were seen between male and female *N. sipedon*. Other studies of *Nerodia* species also showed no differences in movement or home ranges between sexes (Mills et al., 1995; Roe et al., 2004; Pattishall and Cundall, 2008). Although male snakes typically range farther during mating season, some female snakes may move more throughout summer and fall, resulting in larger home range sizes for females of these species (Madsen, 1984; Sperry and Weatherhead, 2009; Hyslop et al., 2014). Home range estimates for *N. sipedon* and other *Nerodia* species from individuals tagged with radio transmitters showed an average use of 210 m to 291 m of stream (Whiting et al., 1997; Pattishall and Cundall, 2008), which is larger than our average estimates for male and female *N. sipedon* and *R. septemvittata*. Several ecological or methodological factors may be responsible for smaller home ranges at our study sites; however, previous studies primarily used radiotelemetry methods to calculate home ranges, which allows for the detection of individuals at significant distance with high probability of detection. Using PIT telemetry, our detections were limited to our sampling transects. Thus, snakes outside of our sampling transects or missed during scanning were not included in our calculations, possibly resulting in an underestimate of home range size. Conversely, a major benefit of PIT telemetry was our ability to monitor hundreds of individuals compared with the small number of individuals monitored in typical radiotelemetry studies. Although PIT telemetry does not provide sufficient detections for an in-depth analysis of home ranges via kernels or minimum convex polygons, estimates generated through SCR and PIT telemetry may assist in examinations of habitat selection both within and across study sites.

Accounting for imperfect detection is a critical part of assessing snake populations (Durso et al., 2011; Ward et al., 2017). We found that detection varied by sex in *R. septemvittata*, with males having higher detection rates than females. Detection rates were also affected by time-varying covariates, with lower detection rates over the course of the season and after rain events for both species. Increased amount of rain between surveys and higher water temperatures decreased detection rates for *R. septemvittata*, possibly as a result of temporary emigration to refuges beyond the detection limit of PIT telemetry. These patterns matched our field observations, as we typically saw more snake activity earlier in the season and less activity after rain events. Previous studies have noted that visual encounters of water snakes can be affected by time of day and year, air or water temperatures, and other environmental covariates (Robertson and Weatherhead, 1992; Lacki et al., 1994; Mills et al., 1995; Burger et al., 2004). Knowing that detection is lower over the course of the season and after rain events is useful for understanding constraints on future surveys or long-term monitoring for the conservation of these species.

The combination of PIT telemetry and SCR analyses for linear habitats was a good match with water-snake ecology and may be useful for other amphibians and reptiles that dwell in structured habitat. First, from a field sampling perspective, the inexpensive cost of PIT tags facilitates marking many individuals and surveying, via PIT telemetry, for marked individuals was relatively efficient. From an analytical perspective, SCR for linear habitats calculates snake movement within streams to determine the linear density of snakes rather than assessing the snakes per hectare as in previous SCR models. Second, by accounting for movement, population density estimates are improved using this approach; not accounting for movement through highly structured areas, such as stream networks, can result in negatively biased population estimates and results that are less representative of an animal's ecology and interactions with the landscape (Sutherland et al., 2015). Finally, density estimates from SCR analyses facilitate comparisons across studies, as the population sizes are directly linked to spatial information (Borchers and Efford, 2008; Muñoz et al., 2016; Sutherland et al., 2016). In contrast, nonspatial capture–recapture analyses often provide the population size, but it is up to the researcher to determine the area in which that population occurs (Borchers and Efford, 2008; Sutherland et al., 2016). Therefore, the nonspatial approach introduces substantial variability to density estimates and makes cross-study comparisons challenging (Muñoz et al., 2016). As such, our approach can be useful to track changes in population density over time and ascertain whether management and conservation actions are needed.

Cooperative Forestry Research Program (accession number 1001968) also provided financial support. All protocols were carried out with approval of the University of Kentucky Institutional Animal Care and Use Committee (identification number 2013-1073).

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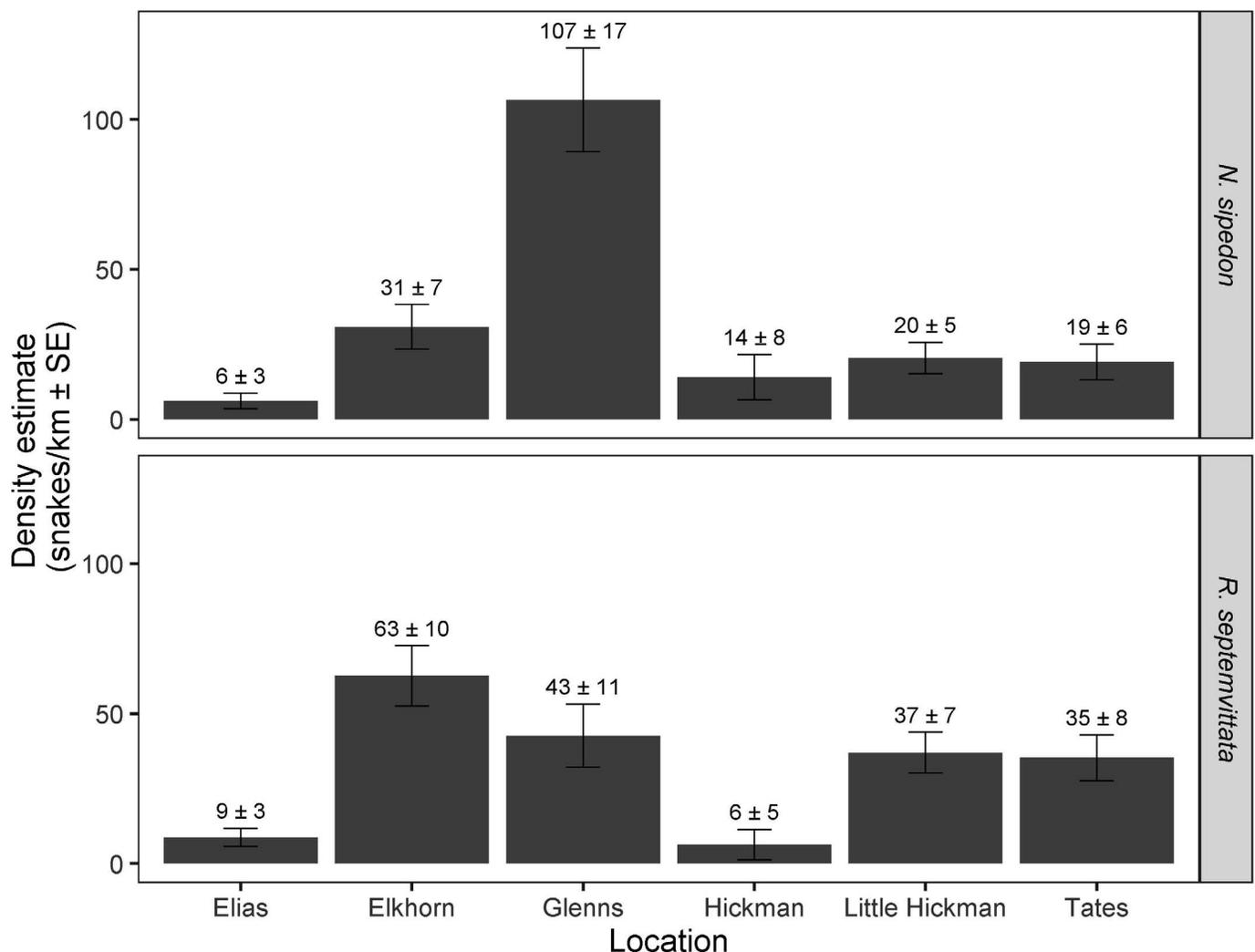
APPENDIX 1

FIG. A1.   Density estimates for *Nerodia sipedon* and *Regina septemvittata* in six central Kentucky streams. Results were based on trap spacing of 30 m between traps. Figure A1 corresponds to Fig. 3, which used a trap spacing of 15 m between traps.
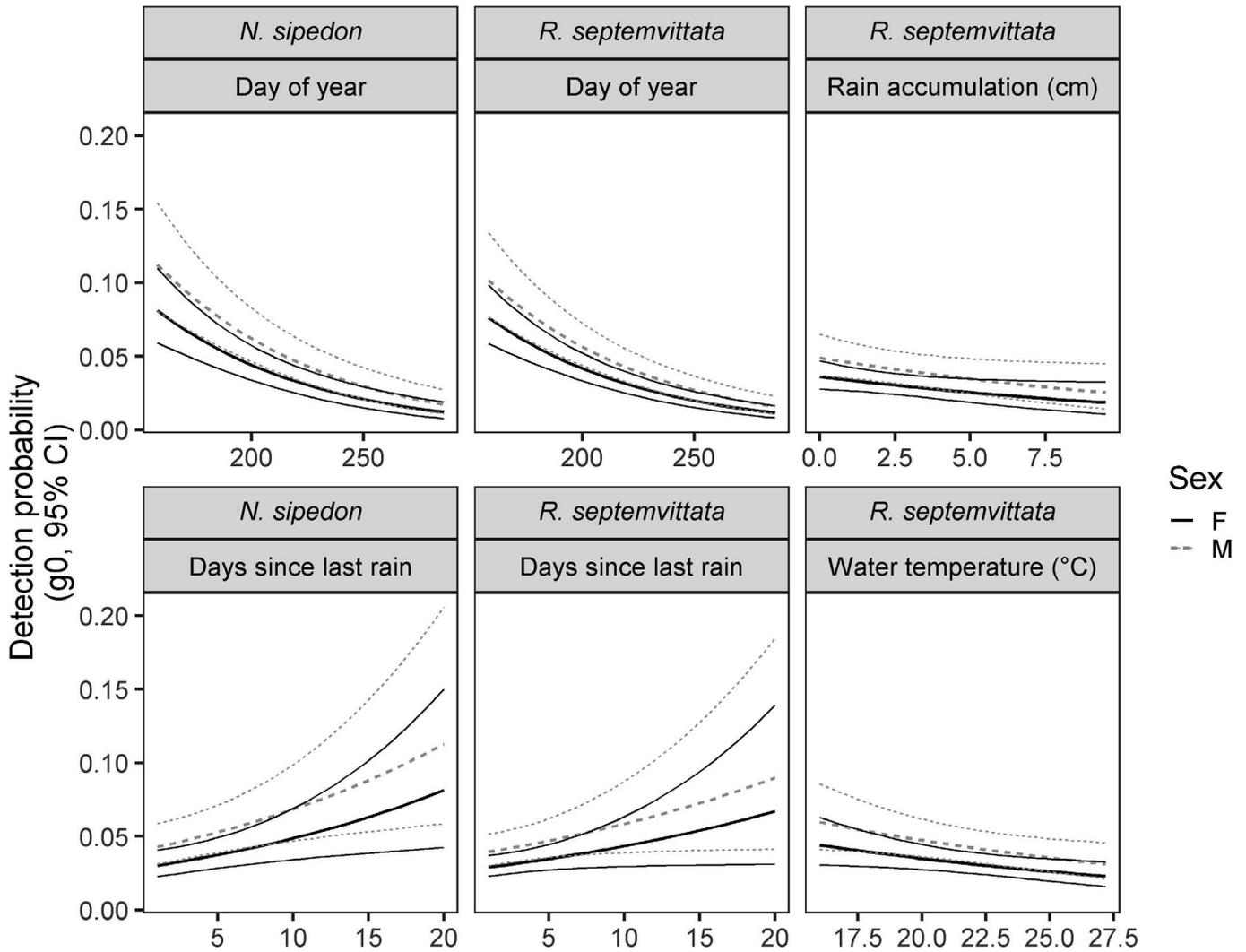
FIG. A2. Detection probabilities of *Nerodia sipedon* and *Regina septemvittata* based on days since last rain, rain accumulation, day of year, and water temperature in central Kentucky between 6 June and 12 October 2016. Solid black lines indicate mean and 95% confidence intervals for female snakes; dashed gray lines indicate mean and 95% confidence intervals for male snakes. Differences among sexes were not significant for *N. sipedon*. Rain accumulation and water temperature were not included in the best model for *N. sipedon* and are not shown. Results were based on trap spacing of 30 m between traps. Figure A2 corresponds to Fig. 4, which used a trap spacing of 15 m between traps.

TABLE A1. Beta coefficients, standard errors (SE), and 95% confidence intervals (CI) for covariates affecting detection (g0) and spatial scale of detection (σ) parameters in spatial capture–recapture analyses for *Nerodia sipedon* and *Regina septemvittata*. Covariates were deemed significant (*) if the 95% confidence intervals did not overlap zero. Results were based on trap spacing of 30 m between traps. Table A1 corresponds to Table 2, which used a trap spacing of 15 m between traps.

Species	Parameter	Covariate	Beta	SE	Lower CI	Upper CI
N. sipedon	Detection (g0)	Sex	0.36	0.21	−0.05	0.77
N. sipedon	Detection (g0)	Days since last rain*	0.17	0.06	0.05	0.30
N. sipedon	Detection (g0)	Day of year*	−0.58	0.08	−0.74	−0.42
N. sipedon	Spatial scale of detection (σ)	Sex	−0.15	0.13	−0.41	0.12
R. septemvittata	Detection (g0)	Sex	0.32	0.18	−0.05	0.68
R. septemvittata	Detection (g0)	Rain accumulation	−0.14	0.07	−0.27	0.01
R. septemvittata	Detection (g0)	Days since last rain*	0.15	0.07	0.00	0.29
R. septemvittata	Detection (g0)	Water temperature*	−0.15	0.06	−0.27	−0.02
R. septemvittata	Detection (g0)	Day of year*	−0.57	0.06	−0.70	−0.44
R. septemvittata	Spatial scale of detection (σ)	Sex*	−0.34	0.12	−0.57	−0.10